Mooij, Wolf M.; Trolle, Dennis; Jeppesen, Erik; Arhonditsis, George; Belolipetsk, Pavel V.; Chitamwebwa, Deonatus B.R.; Degermendzhy, Andrey G.; DeAngelis, Donald L.; De Senerpont Domis, Lisette N.; Downing, Andrea S.; **Elliott, J. Alex**; Fragoso Jr., Carlos Ruberto; Gaedk, Ursula; Genova, Svetlana N.; Gulati, Ramesh D.; Hakanson, Lars; Hamilton, David P.; Hipsey, Matthew R.; Hoen, Jochem 't; Hulsmann, Stephan; Los, F. Hans; Makler-Pick, Vardit; Petzoldt, Thomas; Prokopkin, Igor G.; Rinke, Karsten; Schep, Sebastiaan A.; Tominaga, Koji; Van Dam, Anne A.; Van Nes, Egbert H.; Wells, A.; Janse, Jan H.. 2010 Challenges and opportunities for integrating lake ecosystem modelling approaches. *Aquatic Ecology*, 44. 633-667. 10.1007/s10452-010-9339-3

Challenges and opportunities for integrating lake ecosystem modelling approaches

Wolf M. Mooij[1,*], Dennis Trolle[2] , Erik Jeppesen[2,3], George Arhonditsis[4], Pavel V. Belolipetsky[5], Deonatus B.R. Chitamwebwa[6], Andrey G. Degermendzhy[7], Donald L. DeAngelis[8], Lisette N. De Senerpont Domis[1], Andrea S. Downing[9,1], J. Alex Elliott[10], Carlos Ruberto Fragoso Jr.[11], Ursula Gaedke[12], Svetlana N. Genova[5], Ramesh D. Gulati[1], Lars Håkanson[13], David P. Hamilton[14], Matthew R. Hipsey[15], Jochem 't Hoen[9,1], Stephan Hülsmann[16,17], F.J (Hans) Los[18], Vardit Makler-Pick[19], Thomas Petzoldt[16], Igor G. Prokopkin[7], Karsten Rinke[20], Sebastiaan A. Schep[21], Koji Tominaga[22], Anne A. Van Dam[23], Egbert H. Van Nes[9], Scott A. Wells[24] and Jan H. Janse[25]

1 Netherlands Institute of Ecology (NIOO-KNAW), Department of Aquatic Ecology, Rijksstraatweg 6, NL-3631 AC Nieuwersluis, The Netherlands

2 Aarhus University, National Environmental Research Institute, Department of Freshwater Ecology, DK-8600 Silkeborg, Denmark

3 Greenland Climate Research Centre (GCRC), Greenland Institute of Natural Resources, Kivioq 2, P.O. Box 570 3900, Nuuk, Greenland

4 University of Toronto, Department of Physical & Environmental Sciences, Toronto, ON, M1C 1A4, Canada

5 Institute of Computational Modelling (SB-RAS), Siberian Federal University, 660036, Krasnoyarsk, Russia

6 Tanzania Fisheries Research Institute (TAFIRI), Mwanza Centre, P.O.Box 475, Mwanza, Tanzania

7 Institute of Biophysics (SB-RAS), Akademgorodok, 660036, Krasnoyarsk, Russia

8 University of Miami, Florida Integrated Science Centre, USGS, Coral Gables, FL 33124 USA

9 Wageningen University, Department of Aquatic Ecology and Water Quality, P.O. Box 47, 6700 AA Wageningen, The Netherlands
10 Centre for Ecology and Hydrology, Lancaster, Algal Modelling Unit, Lake Ecosystem Group, Bailrigg LA1 4AP, Lancaster, England, UK
11 Federal University of Alagoas, Campus A.C. Simões, Centre for Technology, 57072-970 Maceió-AL, Brazil
12 Institute of Biochemistry and Biology, Department of Ecology and Ecosystem Modelling, University of Potsdam, Am Neuen Palais 10, D-14469 Potsdam, Germany
13 Swedish University of Agricultural Sciences, Department of Aquatic Sciences and Assessment, P.O. Box 7050, 75007 Uppsala, Sweden
14 University of Waikato, Centre for Biodiversity and Ecology Research, Private Bag 3105, Hamilton, New Zealand.
15 University of Western Australia, School of Earth and Environment, Crawley, WA 6009 Australia
16 Technische Universität Dresden, Institute of Hydrobiology, 01062 Dresden, Germany
17 Technische Universität Dresden, Neunzehnhain Ecological Station, Neunzehnhainer Str. 14, 09514 Lengefeld, Germany
18 Deltares, P.O. Box 177, NL-2600 MH Delft, The Netherlands
19 Technion-Israel Institute of Technology, Faculty of Civil and Environmental Engineering, Technicon City, Haifa 32000, Israel
20 Helmholtz Centre for Environmental Research, Department of Lake Research, Brueckstrasse 3a, D-39114 Magdeburg, Germany
21 Witteveen & Bos, P.O. Box 233, NL-7400 AV Deventer, The Netherlands
22 University of Oslo, Department of Biology, P.O. Box 1066 Blindern, 0316 Oslo, Norway
23 UNESCO-IHE Institute of Water Education, NL-2601 DA Delft, The Netherlands
24 Portland State University, Department of Civil and Environmental Engineering, Portland OR 97207, USA

25 Netherlands Environmental Assessment Agency (PBL), P.O. Box 303, NL-3720 AH Bilthoven, The Netherlands

* Corresponding author (email: w.mooij@nioo.knaw.nl)

Keywords: aquatic; food web dynamics; plankton; nutrients; spatial; lake; freshwater; marine; community; population; hydrology; eutrophication; global change; climate warming; fisheries; biodiversity; management; mitigation; adaptive processes; non-linear dynamics; analysis; bifurcation; understanding; prediction; model limitations

Abstract

A large number and wide variety of lake ecosystem models have been developed and published during the past four decades. We identify two challenges for making further progress in this field. One such challenge is to avoid developing more models largely following the concept of others (‘*reinventing the wheel*’). The other challenge is to avoid focusing on only one type of model, while ignoring new and diverse approaches that have become available (‘*having tunnel vision*’). In this paper, we aim at improving the awareness of existing models and knowledge of concurrent approaches in lake ecosystem modelling, without covering all possible model tools and avenues. First, we present a broad variety of modelling approaches. To illustrate these approaches we give brief descriptions of rather arbitrarily selected sets of specific models. We deal with static models (steady state and regression models), complex dynamic models (CAEDYM, CE-QUAL-W2, Delft 3D-Eco, LakeMab, LakeWeb, MyLake, PCLake, PROTECH, SALMO), structurally dynamic models and minimal dynamic models. We also discuss a group of approaches that could all be qualified as individual-based: super-individual models (Piscator, Charisma), physiologically structured models, stage-structured biomass models, trait-based models and learning type of models like genetic algorithms and neural networks. Thereafter, we zoom in – as an in depth example – on the multi-decadal development and application of the lake ecosystem model PCLake and related models (PCLake Metamodel, Lake Shira Model, IPH-TRIM3D-

PCLake). In the discussion, we argue that while the historical development of each approach and model is understandable given its leading principle, there are many opportunities for combining approaches. We take the point of view that a single 'right' approach does not exist and should not be strived for. Instead, multiple modelling approaches, applied concurrently to a given problem, can help develop an integrated view on the functioning of lake ecosystems. We end with a set of specific recommendations that may be of help in the further development of lake ecosystem models.

Note: citations are temporarily in bold type face so that it easier to check them

Introduction

A large number and wide variety of lake ecosystem models have been developed and published during the past four decades, indicating the strong interest in capturing in a model the essential processes in lake ecosystems (e.g. **Jørgensen 2010**). The scientific interest in understanding fundamental processes in lake ecosystems can be traced back to the seminal paper by **Forbes (1887)** on the lake as a microcosm. Another major purpose has been to develop predictive tools supporting inter-disciplinary ecosystem management **(Carpenter et al. 1999)**, acknowledging the great importance of lake ecosystems for society **(MEA 2005)**. The ecological quality of lakes is threatened by a large number of anthropogenic stress factors, in particular eutrophication, pollution of various types, overexploitation and invasive species, changes in land use and hydrology in the catchment, and climate change (e.g. **Gulati and Van Donk 2002**; **MEA 2005**; **Mooij et al. 2005**; **Revenga et al. 2005**; **MacKay et al. 2009**; **Jeppesen et al. 2009**).

But there is also a downside to the large number and variety of models that have been published. We identify two challenges, one related to the number of models and the other to the variety of models. With respect to the number of models, newly developed models often bear similarities to existing models (*'reinventing the wheel'*) (e.g. **Fitz et al.**

1996). For example, as **Tian (2006)** notes, thirteen functions exist for light forcing on phytoplankton growth, five for nutrient limitation, with similar diversity of other key types of processes. In such cases, it would most likely be more efficient to apply or adopt an existing model instead of creating a new one. With respect to the variety of models, we identify the risk that the approach taken in any specific model is too narrow and ignores other approaches that could be useful or even essential for gaining understanding and making predictions (*'having tunnel vision'*) (e.g. **Scheffer 1998**, p308).

Before starting a lake ecosystem modelling project, it is essential to be aware of existing models and concurrent approaches and to properly conceptualise the issues, the variables, the time and space scales and the desired outcomes for the model simulations (**Robson et al. 2008**). We observe that publications that deal with a wide range of concurrent approaches in lake ecosystem modelling are scarce, although some attempts have been made (**Van Nes and Scheffer 2004**; **Mooij et al. 2009**; **Jørgensen 2010**) and several overviews concerning complex ecosystem models have been provided (e.g. **Schauser and Strube 2007**, **Reichert and Mieleitner 2008**). In this paper we wish to proceed further in the direction of integrating lake ecosystem modelling approaches, without claiming to be comprehensive.

The ideas published here were stimulated by a collaborative research effort by Dutch and Russian scientists funded by a stimulus program of the Netherlands' Organization for Scientific Research and the Russian Foundation for Basic Research. The aim of this research program was to combine the extensive knowledge of the modelling of temperate shallow lake ecosystems of the Dutch team (e.g. **Janse 2005**; **Janse et al. 2008**) with the skilled mathematical knowledge of modelling hydro-dynamic processes of the Russian team (e.g. **Belolipetsky et al. 2010**; **Genova et al. 2010**). The integrated model that resulted from this collaborative research project is documented elsewhere (**Prokopkin et al. 2010**). The aim of the current paper is to compare different modelling approaches and to focus on the potential for combining them either conceptually or technically.

In the first part of the paper a wide range of modelling approaches is presented, each exemplified by – rather arbitrarily selected – existing models. The purpose of this first section is to provide the reader with ideas for potential approaches in lake ecosystem modelling, some of which, we believe, might otherwise be overlooked. In the second part of this paper, we focus on the multi-decadal development and application of a specific lake ecosystem model, PCLake. The aim of this section is to show the potential for expanding and redirecting the approach taken in an existing model. In the final section the barriers and opportunities to integrating lake modelling tools and approaches are discussed, with recommendations for future development directions.

Lake ecosystem modelling approaches

The modelling of lake eutrophication started with empirical models relating total phosphorus (TP) and chlorophyll concentrations, and input-output models relating TP loading and TP concentration (see e.g. **Reckhow and Chapra (1983)** and **Harper (1992)** for overviews). Because of the limitations of static equilibrium models, for instance to predict response times to management measures and to account for the role of sediments and, later, also food web effects, dynamic models for TP and chlorophyll were developed (see overviews by **Chapra and Reckhow (1983)**, **Jørgensen et al. (1995)**, **Jørgensen and Bendoricchio (2001)**, among others). These differ widely in both functional (what compartments are included) and hydrodynamic and spatial aspects (such as 0-, 1-, 2- or 3-dimensional). The inclusion of food web components was also triggered by experiences gained from biomanipulation studies (**Gulati et al. 1990; Benndorf 1995; Hansson et al. 1998; Drenner et al. 1999; Søndergaard et al. 2008**). All these models were developed for phytoplankton-dominated lakes; thus, macrophytes are lacking in many of the models, although the importance of macrophytes to water transparency had been acknowledged by some (e.g. **Spence 1982**; **Chambers and Kalff 1985**) and simple empirical models exist to quantify their effects (**Hamilton and Mitchell 1996, 1997**). In the 1990s, increasing knowledge of the crucial role

of submerged macrophytes and the resulting non-linear behaviour and bistability became available, especially in countries with many shallow eutrophic lakes, such as the Netherlands and Denmark (e.g. **Scheffer 1998**; **Jeppesen et al. 1998**). These phenomena were studied extensively by means of 'minimal dynamic models' (**Scheffer 1998**). Some workers included structural flexibility in dynamic models using optimization criteria (e.g. **Jørgensen 1995, 1999**; **Zhang et al. 2010**). Another modelling line that developed separately was that of physiologically structured models (**Metz and Diekmann 1992**; **De Roos et al. 1992**; **De Roos and Persson 2001**) with applications to zooplankton (e.g. **Hülsmann et al. 2005**) and fish (e.g. **Claessen et al. 2000**), and super-individual models, especially for zooplankton (e.g. **Mooij et al. 2003**), fish (**Van Nes et al. 2002**) and macrophytes (**Van Nes et al 2003**). Yet another development is the use of evolutionary algorithms and neural network models (**Cao et al. 2006**; **Chan et al. 2007**; **Recknagel et al. 2006**) and of fuzzy logic (**Ibelings 2003**) in lake ecosystem models. Many of the different modelling approaches in the literature are mentioned in two recent overviews by **Jørgensen (2008, 2010**). Our study, however, points to an even wider modeling perspective for lake ecosystems and reveals the opportunities for applying and combining different approaches. Below we discuss each of the following approaches in some detail: static models, complex dynamic models, structurally dynamic models, minimal dynamic models, and various individual-based models.

Static models

The classical models of lake eutrophication are the empirical models relating TP and chlorophyll (**Sakamoto 1966** and **Dillon and Rigler 1974** being the pioneers), and the input-output models relating TP loading and TP concentration first derived by **Vollenweider (1968, 1975**) and **Vollenweider and Kerekes (1982)**. These steady state models were the first to use the mass balance approach to lakes. Several modifications were made to these initial models, and the parameters were estimated by regression on multi-lake data sets (e.g. **Dillon and Rigler 1974**; **Kirchner and Dillon 1975**; **Jones and Bachmann 1976**; **Larsen and Mercier 1976**; **Reckhow 1979**; **Canfield and Bachmann 1981**; and others; see e.g.

191 **Reckhow and Chapra (1983)** and **Harper (1992)** for overviews). These models allow
192 calculations of average nutrient and chlorophyll concentrations (and sometimes
193 transparency) given P and N loading and some basic lake features, of which mean depth,
194 and retention time have proven to be the most important. Nutrient loading criteria, together
195 with uncertainty bounds (**Reckhow and Chapra 1983**), were derived for the classification of
196 lakes in different trophic states (ultra-oligotrophic, oligotrophic, mesotrophic, eutrophic or
197 hypertrophic). These states could be defined both in terms of TP, TN and chlorophyll
198 concentrations or transparency and also in terms of characteristic species composition. This
199 type of model is still useful (and is being used) for giving a first estimate of the effects of
200 eutrophication on lakes. Other simple regression models include relationship between TP,
201 TN and/or lake depth versus, respectively, bird numbers and richness (**Hoyer and Canfield**
202 **1994**), fish biomass and/or production (**Hanson and Leggett 1982**; **Downing et al. 1990**;
203 **Randall et al. 1995**; **Bachmann et al. 1996**), zoobenthos biomass **(Hanson and Peters**
204 **1984)**, macrophyte coverage and plant volume present **(Bachmann et al. 2002;**
205 **Søndergaard et al. 2010)**, zooplankton biomass **(Hanson and Peters 1984; Jeppesen et**
206 **al. 1997, 2005)**, zooplankton:phytoplankton biomass ratio **(Jeppesen et al. 2005)** and
207 phytoplankton biovolume at the class level **(Downing et al. 2001; Jeppesen et al. 2005;**
208 **Håkanson et al. 2007)** and bacterioplankton biomass and production **(Hardy et al. 1986;**
209 **Roland et al. 2010)**. Some empirical models have linked measures of biodiversity (e.g.,
210 species richness or richness of native species) in lakes to external factors **(e.g. Leibold**
211 **1999; Jeppesen et al. 2000; Alkemade et al. in press)**.
212 The advantages of these models are that they are simple and easy to use, they
213 provide general relationships, they are based on a large amount of data from lakes with
214 different trophic states and they implicitly account for the net effect of structural changes
215 along the nutrient gradient, which are often difficult to include in more complex dynamic
216 models. These simple regression models have, therefore, been extensively used by water
217 quality managers world-wide for setting targets for acceptable nutrients and, not least, TP

loading to lakes. Their disadvantage is that the coefficient of variation in the predictions is generally high and individual lakes may follow trajectories deviating from the general pattern.

Complex dynamic models (examples given in alphabetical order)

CAEDYM

The Computational Aquatic Ecosystem Dynamics Model (CAEDYM) is a process-based library of water quality, biological and geochemical sub-models that is driven by either the Dynamic Reservoir Simulation Model (DYRESM: 1D Lagrangian vertical stratification model) or the Estuary and Lake Computer Model (ELCOM: 3D structured grid hydrodynamics model) to account for transport and mixing. Both DYRESM and ELCOM have been applied widely to investigate stratification in lakes and drinking water reservoirs and inflow/outflow dynamics of the waterbodies (**Robson and Hamilton 2003; Hamilton 1999**). The most recent version of CAEDYM (v3.3, **Hipsey and Hamilton 2008**) can also model suspended solids, oxygen and organic and inorganic nutrients (C, N, P and Si), multiple phytoplankton functional groups, zooplankton and fish, benthic biological communities (macroalgae, macrophytes and benthic invertebrates), pathogens, geochemistry (including ions, pH, redox and metals), and sediment oxygen, nutrient and metal fluxes. These are represented by a long series of mass-conservative coupled differential equations, but the ecosystem representation is configurable and can be varied by the user depending on the purpose of the model and the availability of data. For long-term simulations DYRESM-CAEDYM has been widely used (e.g., **Bruce et al. 2006**; **Burger et al. 2007**; **Trolle et al. 2008a, b**; **Gal et al. 2009**), but when higher spatial resolution is required due to the importance of more complex horizontal circulation and transport processes, ELCOM-CAEDYM is more suitable (**Hipsey et al. 2008**; **Chung et al. 2009**; **Leon et al. in press**). CAEDYM has been used widely for studying nutrient cycling, the effects of increased nutrient loading on algal blooms and changes to phytoplankton succession, as well as for identifying conditions that favour cyanobacteria (**Wallace and Hamilton 2000; Lewis et al. 2004**). CAEDYM is also able to resolve bacteria as a discrete ecosystem component and this has been shown to be

246 important to represent the dynamics of micro-grazers and the 'microbial loop' (**Gal et al.**
247 **2009**).
248
249 *CE-QUAL-W2*
250 CE-QUAL-W2 is a two-dimensional laterally-averaged hydrodynamic and water quality
251 model that simulates vertical stratification and longitudinal variability in key ecosystem
252 properties. The current model (v3.6, **Cole and Wells 2008**) can simulate suspended solids,
253 nutrient and organic matter groups, residence time, derived variables such as TN, TKN,
254 TOC, Chl a, as well as pH, total dissolved gases and optional biotic groups, including
255 multiple periphyton, multiple phytoplankton, multiple zooplankton, and multiple macrophyte
256 groups interacting with hydrodynamics (**Berger and Wells 2008**). The model includes
257 various vertical turbulence closure, weirs/spillways, gates, pipes, and pumps and reaeration
258 schemes for engineered systems, which can be simulated depending on the nature of the
259 water body. The model is an open-source code written in FORTRAN. It has been used
260 extensively throughout the US (e.g., **Deliman and Gerald 2002**; **Bowen and Hieronymous**
261 **2003**; **Debele et al. 2006**) and elsewhere in the world (e.g., **Chung and Oh 2006**; **Kuo et al.**
262 **2006, 2007**) as a management and research tool, particularly for studying the nutrient and
263 sediment dynamics of reservoirs and river impoundments. The model has also been used to
264 drive models of food web dynamics (**Saito et al. 2001**), and to support studies of fish habitat
265 (**Sullivan et al. 2003**). Despite the model's complexity, it has also been subject to advanced
266 calibration procedures (**Ostfeld and Salomons 2005**).
267
268 *Delft 3D-Eco*
269 Delft3D is a 2D/3D modular modelling system to investigate hydrodynamics, sediment
270 transport, morphology and water quality for lake, fluvial, estuarine and coastal environments.
271 The FLOW module is the heart of Delft3D and is a multi-dimensional (2D or 3D)
272 hydrodynamic model that calculates non-steady flows and transports resulting from tidal and
273 meteorological forcing on a curvilinear, boundary-fitted grid. This allows one to align the

grids with curving boundaries and channels and to concentrate the higher resolution in areas of interest. The sediment module Delft3D-SED simulates the inorganic sediment behaviour in the water and at the bed (transport, sedimentation, resuspension) as a function of discharges, sediment characteristics and waves, and is widely applied to simulate suspended matter in shallow lakes. The ecological module (Delft3D-ECO) is always applied in conjunction with the water quality module (Delft3D-WAQ). Included in Delft3D-ECO are physical, biological and/or chemical reactions. These processes are related to algae growth and mortality, mineralization of organic matter, nutrient uptake and release, and oxygen production and consumption. The Delft3D-ECO modelling instrument considers three nutrient cycles: nitrogen, phosphorus and silicon. The carbon cycle is partially modelled, with a mass-balance of all components containing organic carbon. Phytoplankton kinetics are simulated by the model BLOOM, which is based on a competition principle using the ratio between the actual growth rates and the resource requirements **(Los, 2009).** The model maximises the net production of the phytoplankton community in a certain time period consistent with the environmental conditions and existing biomass levels by use of an optimisation technique called linear programming. Algal diversity in freshwater applications is represented in three species groups: diatoms, flagellates and green algae and three genera of cyanobacteria: Microcystis, Aphanizomenon and Planktothrix. To model variable stoichiometry, each group is represented by three types defined by physiological state of the phytoplankton: phosphorus-, nitrogen- or light-limitated. The model can easily be extended to extra groups/species of phytoplankton or freshwater or marine macro algae using characteristics stored in a large data base. Different formulations are available for characterisation of grazers, microphytobenthos, bottom sediment and sediment-water exchange. The most comprehensive description of the model and notes on the historical development of Delft 3D-Eco and some of its forerunners can be found in **Los (2009, chapter 7**).

Ecopath with Ecosim

ECOPATH (**Christensen and Pauly 1993**) is an ecosystem mass-balance model for creating static snapshots of food webs, where functional groups are represented as biomasses, linked through their trophic interactions. The model establishes mass-balances by solving sets of linear equations that describe the production and consumption of each group. ECOPATH has reasonably low data requirements, and single mass balances give valuable insights to how energy is transferred through a system. Multiple balances are used for temporal or spatial comparisons of system functioning. The time-dynamic module ECOSIM (e.g. **Li et al. 2010**) applies differential equations to describe temporal variations of the flows identified by ECOPATH mass-balances and is mostly used to study effects of fisheries' management policies in both marine and freshwater systems. ECOPATH is especially useful during the initial stages of investigations on a specific lake ecosystem because setting up and balancing models can unveil inconsistencies in source-data and inspire the development of hypotheses for further research.

LakeMab

Process-based models like LakeMab quantify fundamental transport processes in lakes, such as inflow, outflow, sedimentation, resuspension, diffusion, biouptake and retention in different types of biota, mixing, substrate decomposition, etc. The basic aim of this modelling is to find general functions for these transport processes that may be applied for all or, at least, most types of lakes, coastal systems and for most types of substances with a particulate phase. LakeMab has been tested for phosphorus, suspended particulate matter (**Håkanson 2006**), radionuclides and metals (see **Håkanson 2000**).

LakeWeb

Lake Web is a general model to quantify lake foodweb interactions, including biotic/abiotic feedbacks (**Håkanson and Boulion 2002**). The model has been tested against empirical data sets, mainly from Europe. It includes the following functional groups of organisms: phytoplankton, bacterioplankton, benthic algae, macrophytes, zoobenthos, herbivorous and

predatory zooplankton, prey fish and predatory fish. It uses ordinary differential equations and gives weekly variations in production and biomass for nine groups of organisms. Fundamental concepts include consumption rates, metabolic efficiency ratios, distribution coefficients, migration of fish and predation pressure. An important feature of LakeWeb is that it can be run by just a few driving variables readily accessible from standard maps and monitoring programs. Several scenarios for management issues such as the consequences of biomanipulation, changes in land-use, eutrophication, acidification and global temperature changes are available. LakeWeb can simulate such measures and predict the positive and negative consequences of remedial measures. The present version of LakeWeb has been tested for lakes smaller than 300 km^2, but many of the structural components should be valid also for larger systems, e.g., for coastal areas or the large lakes of the world.

MyLake

MyLake (MultiYear Lake) is a 1-dimensional lake model code that simulates daily changes in physical and chemical dynamics over the depth gradient, including surface radiation balance, vertical light attenuation,vertical temperature and density profiles, ice and snow cover, and phosphorus exchange between suspended particles and water, as well as between water and sediment (**Saloranta and Andersen 2007**). The modelling principle is mostly based on MINLAKE (**Riley and Stefan 1988**) with some adjustments and additions. In particular, incorporation of ice and snow dynamics based on physical processes (**Leppäranta 1993**; **Saloranta 2000; Salonen et al. 2009**) gives the model code additional utility for boreal lakes. MyLake has been applied to lakes in Norway (**Lydersen et al. 2003**; **Saloranta 2006**) and Finland (**Kankaala et al. 2006**; **Saloranta et al. 2009**).

PCLake

PCLake is an integrated ecological model of shallow non-stratifying lakes, describing phytoplankton, macrophytes and a simplified food web, within the framework of closed nutrient cycles. Its aim is to analyze the probability of a transition from the vegetation-dominated clear-

water state to the phytoplankton-dominated turbid state, or vice versa, as a function of the external nutrient loading and other factors. Both bottom-up, top-down and indirect effects are included. PCLake has been designed to simulate the main nutrient and food web dynamics of a non-stratifying lake in response to eutrophication and related restoration measures (**Janse et al. 1992, 1995, 2008, 2010**; **Janse and Van Liere 1995**; **Janse 1997, 2005**). The model describes a completely mixed water body and comprises both the water column and the sediment top layer (10 cm), with the most important biotic and abiotic components (Fig. 1). The upper sediment layer is included, to take into account sediment-water exchange and deposition history. Optionally, a wetland zone with helophytes can be added (Fig. 2). No further horizontal (like depth variations) or vertical distinction within the lake is taken into account. Mathematically, the model is composed of a number of coupled differential equations, one for each state variable. All biota are modelled as functional groups. The main groups in the water phase are three groups of phytoplankton (diatoms, greens and cyanobacteria), zooplankton, planktivorous, benthivorous and piscivorous fish. Submerged macrophytes are included, consisting of a shoot and a root fraction. Further groups in the top layer of the sediment are the settled fractions of the three types of phytoplankton, as well as zoobenthos.

Closed mass balances throughout the model system were attained by modelling each compartment in three components, namely, dry weight as a surrogate for carbon, nitrogen and phosphorus. Additionally, diatoms and detritus are described in silicon (Si). Inorganic carbon (CO_2) is not explicitly modelled. Oxygen in the water column is modelled dynamically, while sediment oxygen is described by a simpler approach that still accounts for oxygen influence on nutrient release. The nutrient-to-dry weight ratios are thus variable. As the stoichiometry of organisms changes with trophic level, mechanisms are included to allow for those differences, such as a higher assimilation efficiency for nitrogen and phosphorus than for carbon. Apart from mass fluxes, the model also contains some empirical relationships to represent indirect effects between two groups of organisms, such as the impacts of fish and macrophytes on resuspension. For a detailed description of all processes see **Janse (2005)**. The model has

been used to estimate the critical nutrient loading levels for both forward and backward switch between the clear and the turbid state of shallow lakes, and to identify the key processes determining the switch and the way these levels depend on lake features and management factors (**Janse et al., 2008**). In the second part of this paper we will look at PCLake in more detail.

PROTECH

PROTECH (Phytoplankton RespOnses To Environmental Change) simulates the dynamic responses of up to 10 species of phytoplankton (from a library of over 100) to environmental variability in lakes and reservoirs. The model calculates exponents describing growth and loss processes (mortality, sedimentation, consumption by grazing zooplankton), on the basis of the maximum growth rates of algal species in culture. A key characteristic of PROTECH is the use of morphological traits of phytoplankton, which enable the key physiological parameters (growth rates etc) to be parameterized according to defined threshold levels of light, temperature and nutrients. The model was been extensively applied as evident from over 30 peer-reviewed publications (see **Elliott et al. 2010** for a review). Its formulation and equations are presented in **Reynolds et al. (2001)**.

SALMO

SALMO (Simulation of an Analytical Lake Model, **Benndorf and Recknagel 1982**) is intended to simulate the most important planktonic food-web compartments of lakes and reservoirs. The original version and the “basic version” SALMO-II consist of two layers (epilimnion and hypolimnion) with variable mixing depth. In comparison to other models the equations and parameters of SALMO are intended to be rather general, so that site-specific calibration can be avoided or at least limited to few site-specific parameters only (e.g. light extinction, sediment P-release, fish stock). If horizontal exchange rates are available (e.g. from a hydrodynamic 3D model) multiple horizontal compartments can be combined. The recent version SALMO-HR is a vertically resolved 1D hydrophysical-ecological coupled

model, which consists of the ecological sub-model SALMO-1D (**Rolinski et al. 2005, Petzoldt et al. 2005, Baumert et al. 2005**) and the hydrophysical k-ε-model LAKE (**Baumert et al. 2005**). It simulates the seasonal development of temperature, stratification and turbulence (physical components) as well as the concentrations of phosphorus, nitrogen, phytoplankton (three or more functional groups), zooplankton, oxygen, DOC (with a focus on humic substances) and suspended matter (4 particle classes). The model is used for scenario analysis (e.g. **Petzoldt and Uhlmann 2006**), in decision making and as a research tool.

Structurally dynamic models

As stated in **Zhang et al. (2010)**: “In structurally dynamic models, the parameters are constantly varied to account for adaptations and shifts in the species composition. Changes in the parameters are based on either expert knowledge or optimization of a goal function that can describe the fitness under changing environmental conditions. This approach attempts to overcome the weaknesses associated with traditionally used models: (1) Fixed and rigid parameter sets are used in such models, which can hardly reflect the changes in species properties and compositions according to the prevailing conditions of the ecosystem and (2) calibration is often difficult, because we have to deal with a number of uncertain parameters simultaneously and test them within a wide range of possible values.” A comparable approach using “dimensionless moderators” was proposed by **Håkanson and Peters (1995)**.

Minimal dynamic models

Like the static models minimal dynamic models are very simple. The difference with static models is that they describe changes through time and consist of a few differential or difference equations that focus on a single aspect of a system, based on clear assumptions (**Van Nes and Scheffer 2004**). These kind of models are also called ‘strategic’ (**Levins 1966**) or sometimes ‘conceptual’ (**Grimm 1994**).

Simple models often generate a hypothesis about a possible cause of a phenomenon that would not easily be achieved intuitively (**Scheffer and Beets 1994**). These models are more popular among fundamental scientists than lake managers, as they aim more at development of theory and understanding of complex lake systems rather than making realistic predictions. Even if the results are unrealistic we can still learn much from these models, as they may point to other mechanisms that are essential but lacking in the simple model. These models have the advantage that their behaviour can usually be explored completely with well-tested software tools for bifurcation analysis (**Kuznetsov 1995**). A subset of the simplest minimal models can even be analyzed mathematically. The main disadvantage is that minimal models obviously focus on only one aspect of the ecosystem, while in reality the underlying causation may be much more complex (**Scheffer and Beets 1994**). Furthermore, these approaches may set artificial constraints to the level of abstraction, not dictated by nature but by the available mathematical analysis tools. Minimal dynamic models have been developed to study non-linear dynamics between predator and prey (e.g. Scheffer et al. 1997) but also to study spatial pattern formation in predator-prey interactions (e.g. De Roos et al. 1991).

While being a conceptual instead of a dynamic model, PEG (Plankton Ecology Group) model (**Sommer et al. 1986**) of seasonal planktonic succession in temperate lakes can be considered to be a minimal model. The strong impact of this model (measured by the numerous times it is cited) shows the potential of minimal models to provide conceptual insights into lake ecosystem dynamics. Subsequently, minimal dynamic models of seasonal succession have been developed (**Scheffer et al. 1997**) and these now also have been used for evaluating the impact of climate change on lake ecosystems (e.g. **Scheffer et al. 2001a**; **Van Donk et al. 2003**; **De Senerpont Domis et al. 2007**). It is important to notice that these models, due to being simple, can only give conceptual answers and should be used with great caution, e.g. when predicting the effects of climate change (**Jeppesen et al. 2003**).

Individual-based models

In many ecological systems knowlegde of the variation in size of individuals is essential (**Huston et al. 1988**), for instance in fish populations where size is essential for survival (**Mooij 1996**) and also for macrophyte populations that compete for light based on their elevation in the water column. To model such populations accurately we need to consider individual traits or even individuals separately. This individual-based approach has become popular among ecologists, as it may produce realistic patterns (for instance length distributions of fish) that can be checked with field data (**Grimm et al. 2005**). As far as we know, it has not yet been applied in full-scale ecosystem models. Instead, individual-based models usually focus on a few ecological groups. For modelling large populations in lakes, it is generally too computationally demanding to model all individuals separately (individual-based model *sensu stricto*). Three computationally more efficient approaches are presented below, the super-individual approach (**Scheffer et al. 1995**), physiologically structured models (**De Roos et al. 1992**) and stage-structured biomass models (**De Roos et al. 2008**). The latter approach could equally well be categorized as a minimal dynamic model and provides a nice bridge between individual-based approaches and simple, unstructured models of consumer-resource interactions in aquatic systems. Trait-based models may be regarded as a subset of individual-based models. Here, the average value of traits vital to the functioning of the food web (e.g. body size, edibility, selectivity, or carbon to nutrient ratios) is modelled dynamically, using either ordinary or partial differential equations.

Super-individual models

The super-individual approach starts with developing an individual-based model, in which individuals are modelled separately. These individuals differ in their characteristics (e.g. size, weight, age). In the super-individual approach each individual has an extra property, namely the number of individuals that it represents. Mortality can modelled as drawing from binomial distributions. It can easily be used in combination with a discrete event queue, which is sometimes used in individual-based models (**Scheffer et al. 1995**). This approach is closely

498 related to that of physiologically structured models, but the implementation differs and it is
499 easier to scale down to a truly individual-based approach when modelling small populations
500 (**Scheffer et al. 1995**).
501 The approach has been applied to the macrophyte model Charisma (**Van Nes et al. 2003**)
502 and the fish model Piscator (**Van Nes et al. 2002**). In both models competition between
503 many species can be modelled. Charisma describes the seasonal cycle of macrophytes in
504 temperate regions. Moreover, it is (optionally) spatially explicit. It is especially detailed in the
505 description of photosynthesis, and can model self-shading and shading among different
506 species. The model can have alternative stable states for different reasons (**Van Nes et al.**
507 **2003**). A truly individual-based version has been employed to describe in detail clonal growth
508 of *Potamogeton perfoliatus* in a very detailed way (**Wolfer et al. 2006**).
509 Piscator has, as a default, eight interacting fish species, three types of fishery (fykes,
510 seine and gill nets), piscivorous birds and a simple representation of the fish food
511 (zooplankton, benthos), but one can add as many user-defined species as required. The
512 model can include size differences among year-classes by defining different super-
513 individuals with slightly different growth rates. Feeding is modelled in an especially detailed
514 way. Special attention has been paid to controlling complexity of the model. Therefore the
515 model is very flexible and it is possible to zoom in or out on different processes by removing
516 species without changing the computer code. Furthermore an option has been implemented
517 to shut down feedback mechanisms between predators and prey. This way the complexity
518 can be increased gradually, which makes calibration easier (**Van Nes et al. 2002**), though
519 caution should still be excercised in the knowledge that parameter values may change with
520 the inclusion of different state variables.
521
522 ***Physiologically structured models***
523 As stated in **De Roos and Persson (2001**): “Physiologically structured population models
524 offer a concise framework to explicitly and mechanistically relate population-level
525 phenomena to individual-level processes, in cases where the former are significantly

influenced by physiological (e.g. size) differences among individuals. Central to PSPMs is the clear distinction between the individual and its environment and the strict separation of the individual and population level. The model formulation process consists of the derivation of a mathematical description of how individual performance (growth, survival, reproduction) relates to the physiological characteristics of the individual and the condition of its environment. Hence, all assumptions about and parameterisation of these functional relationships in response to its current environment take place exclusively at the level of a single individual organism. The derivation of the population model is subsequently only a matter of book-keeping without making any further assumptions." While accounting for age or size (known to be of paramount importance for physiological processes) in physiologically structured models as a major distinction to unstructured models, the fact that dynamic energy budgets (**Kooijman 2000, Baird & Suthers, 2007**) are obeyed implies that all traits are linked. Thus all individuals of the same size or age are assumed to be identical. On the one hand this keeps the model mathematically tractable and allows, e.g., the quantification of trade-offs (**Rinke et al. 2008**), while on the other hand the linkage of traits makes these models less suited for including genotypic or phenotypic plasticity as in truly individual-based approaches.

Stage-structured models

As stated in **De Roos et al. (2008**) "the model, which we refer to as the stage-structured biomass model, is formulated in terms of a set of ordinary differential equations. Nonetheless, under equilibrium conditions the model predictions are identical to those of a physiologically structured population models accounting for a continuous size-distribution, from which the stage-structured biomass model is derived. Under these conditions the model therefore consistently translates individual life history processes, in particular food-dependent growth in body size, to the population level." An advantage of stage-structured biomass models over physiologically structured models is their mathematical tractability.

554 ***Trait-based models***

555 The high diversity encountered at different hierarchical scales enables ecological systems to
556 adapt to the prevailing conditions (e.g., by shifts in functional types, species, clones and
557 genotypes), which often also buffers their responses to perturbations (**Gunderson 2000**).
558 Allowing for such potential to adapt, strongly alters the dynamic behaviour of lab food webs
559 and their model representations (**Yoshida et al. 2007**). Hence, neglecting the naturally
560 existing functional diversity and potential to adapt in lake models, may strongly reduce their
561 realism and predictive power. One approach to consider this potential for adaptation in
562 mathematical models is to split up one or more functional group into several subunits which
563 differ in their parametrization (e.g. **Vos et al. 2002**; **Tirok and Gaedke 2010**). The choice of
564 parameters may follow trade-offs between the different functional traits the importance of
565 which becomes increasingly recognized (**Litchman et al. 2007**). This reduces, but does not
566 alltogether avoid, the increase in the number of free parameters.

567 Alternatively, the number of functional groups can be kept small when their
568 parameterization varies in time depending on ambient conditions. Such trait-based modelling
569 approaches depict species (or functional groups, clones, genotypes, etc.) or sizes by their
570 functional traits and the corresponding trait values (e.g. **Wirtz and Eckhardt 1996**; **Norberg**
571 **2004**; **Savage et al. 2007; Harris 2006; Baird and Suthers 2007**). A continuous trait value
572 distribution describes the relative importance of the functionally different units, where the
573 mean trait value reflects the strategy of the most abundant units and the variance the
574 functional diversity. The trait value distribution may continuously change when growth
575 conditions are altered, which reflects an increase in the share of species better suited for the
576 current environment (**Wirtz and Eckhardt 1996**; **Merico et al. 2009**). Adaptive dynamics
577 have been employed to study predator-prey coevolution (e.g., **Abrams and Matsuda 1997**)
578 and increasingly also community dynamics and their potential to adapt to environmental
579 changes (**Norberg 2004**; **Savage et al. 2007**). The multi-species and dynamic trait approach
580 give similar results when based on comparable assumptions (**Merico et al. 2009**).

So far, models describing the ability of community dynamics to adapt have been restricted to one trophic level (mostly primary producers, e.g., **Wirtz and Eckhardt 1996**; **Norberg 2004**) or at most two trophic levels (**Abrams and Matsuda 1997**; **Tirok and Gaedke 2010**). An extension to complex multitrophic level food webs represents a future challenge, given the rise in model complexity and the uncertainties in the trade-off functions. A coarse, non-mechanistic but simple approach potentially suitable for complex food web models may be to extend the functional response using a term for predator interference which might mimic, e.g., increasing prey defence at high predator densities.

Use of hybrid evolutionary algorithms, neural networks

The hybrid evolutionary algorithm (**Cao et al. 2006**) was designed to uncover predictive rules in ecological time-series data. It combines genetic programming to generate and optimise the structure of rules,and genetic algorithms to optimise parameters of rules (e.g. **Recknagel et al. 2006**). Resulting rules are subsequently evaluated by means of fitness criteria, where fitter rules are selected for recombination to create the next generation by using genetic operators such as crossover and mutation. These steps are iterated over consecutive generations until the termination criterion of the run has been satisfied and the fittest rule has been determined. A detailed description of the design and functioning of HEA, including a demo software version, are provided by **Cao et al. (2006)**.To determine generic rule-based agents for each lake category HEA is imbedded in a k-fold cross-validation framework (**Kohavi 1995**) based on k-fold data partitioning and the consecutive use of each part of the data for both training and validation. This method has, for example, been used for a number of lakes, resulting in rule-based agents for forecasting 5- to 7- days-ahead abundances of *Microcystis* in the shallow-polymictic and hypertrophic lakes in Japan, in warm-monomictic and hypertrophic lakes in South Africa and abundances of *Oscillatoria* in two shallow lakes in the Netherlands (**Recknagel et al. 2006**).

Use of Kalman filters and fuzzy logic

609 Most of the models described here were mainly designed for seasonal applications. From a
610 management point of view there is also a demand for (near) real time forecasting, for
611 example, of cyanobacterial blooms in lakes used for recreation. The accuracy of traditional
612 models in predicting this type of event is usually not very high, however. An improvement
613 may be obtained by a combination of different techniques, as was already described in the
614 previous section. As an alternative, Kalman filters and fuzzy logic are also applied in real
615 time forecasting systems of phytoplankton blooms. Kalman filters are applied in conjunction
616 with deterministic equations to improve the accuracy of predictions based on systematic
617 discrepancies between modelled and observed conditions. They have been widely applied in
618 predicting storm surges, high water events or weather forecasts, which are often difficult to
619 predict by models that are basically designed for simulating average conditions. Examples of
620 existing applications for phytoplankton predictions in marine systems are given in **Allen et**
621 **al. (2003)** and **Mao and Lee (2009)**.
622 Fuzzy logic provides another technique to improve the predictive power of
623 deterministic models. In this case certain processes, which cannot be easily described by
624 deterministic equations, are modelled using knowledge rules. As an example consider 'if the
625 average wind speed is less than 4 m s^{-1} and the irradiance is high, then there is a high
626 probability that a surface bloom of cyanobacteria is formed'. The fuzzy rule-based models
627 are often employed to capture the approximate mode of reasoning that plays an essential
628 role in dealing with uncertain and imprecise data. The fuzzy logic theory is based on an
629 extension of the classical meaning of the term 'set' and formulates specific logical and
630 arithmetical operations for processing imprecise and uncertain information. The main
631 application areas of the fuzzy set theory in ecological research are data analysis,
632 knowledge-based modelling and decision making (**Salski and Holsten 2006**). A combined
633 application of fuzzy logic with the deterministic Delft3D-ECO model to describe the formation
634 and horizontal distribution of surface water blooms of toxic cyanobacteria is given by
635 **Ibelings et al. (2003)**. **Laanemets et al. (2006)** use fuzzy logic to predict cyanobacteria

636 blooms of *Nodularia* in the Baltic, **Blauw et al. (2010)** use fuzzy logic to predict foam on
637 beaches.
638
639 ## PCLake as an in-depth example
640 In this section, we describe in-depth, as an example, the multi-decadal development of the
641 model PCLake, and the way it has been applied and linked to different model approaches.
642 We chose this model, because several of the authors are familiar with it and were engaged
643 in its development, and because it nicely illustrates the challenges met and the choices to be
644 made when developing a model over several decades in response to changing management
645 questions. Other models could have served as an example equally well.
646 First we describe the model development and applications, including uncertainty
647 analysis and some comparisons with other models. Secondly, we describe a metamodel
648 derived from the dynamic model, and thirdly, the links that have been made with other
649 approaches (namely, coupling with hydrodynamic models and with empirical biodiversity
650 relations). We conclude with apparent limitations of the model and ways to cope with these.
651
652 ***Model development and applications***
653 As stated before, PCLake has been designed to simulate the limiting nutrient, phytoplankton
654 and food web dynamics of a non-stratifying lake in response to eutrophication and to
655 restoration measures (**Janse 1997, 2005**). The first version (then called PCLoos) was
656 developed within the Lake Loosdrecht Water Quality Project (WQL), a shallow peat lake in
657 the Netherlands (**Van Liere and Janse 1992**; **Janse et al. 1992**). This project aimed to
658 elucidate the mechanisms causing the algal bloom problems in the lake and to estimate the
659 effects of reduction in phosphorus loading and other restoration measures such as dredging,
660 P fixation and biomanipulation. The model focused on phosphorus as nutrient, the three
661 main algal groups present, the sediment top layer (because of the intensive exchange
662 between water and sediment in the lake) and top-down effects on the algae via zooplankton

663 and fish. The choice was made to develop a model of 'intermediate' complexity, covering the
664 broad ecological structure of the system, with limited chemical and hydrodynamical details
665 compared to the existing models of the time. Variable P/C stoichiometry throughout the
666 system was included from the start, based on field and experimental data from this and other
667 lakes. The model correctly simulated that the proposed P reduction measure did not stop the
668 algal bloom and indicated the causes of the failure (such as decrease of the P/C ratio)
669 (**Gulati et al. 1991; Van Liere and Janse 1992**). Scientific and management interests in the
670 'alternative stable states' concept triggered an extension of the model (now called PCLake)
671 with macrophytes, predatory fish and a nitrogen cycle, in order to cover both states of the
672 system (the current 'turbid' and the desired 'clear' state). The model proved, indeed, to be
673 able to produce switches between clear and turbid states, and to mimic hysteresis effects
674 (**Janse 1997**; **Janse et al. 2008**) and the effects of biomanipulation (**Janse et al. 1995**).
675 Management interests also triggered the development of a wetland module allowing
676 simulation of the impacts of helophytes zones for lake restoration (**Janse et al. 2001**; **Sollie**
677 **et al. 2009**), hence taking into account a (limited) spatial aspect. Technically, the model was
678 originally implemented in the simulation package ACSL/Math (**Aegis 2001**), including a
679 MATLAB-like user interface apt for batch calculations. Later, a freely distributed OSIRIS
680 (**Mooij and Boersma 1996**) version was made, consisting of a C++ executable called from
681 an MS Excel shell.

682 The model has been tested by a sensitivity analysis (by methods suited for non-linear
683 models) and a Bayesian parameter estimation and uncertainty analysis comparable to GLUE
684 (**Janse et al. 2010**). After identifying the key sensitive parameters, these were calibrated on
685 the combined data on total phosphorus, chlorophyll-a, macrophyte cover and Secchi depth
686 in over 40 lakes. This was done by a Bayesian procedure, giving a weight to each parameter
687 setting based on its likelihood (**Aldenberg et al. 1995**). This procedure hence aimed at an
688 overall best fit for the whole sample of lakes rather than an optimal fit for one lake at the
689 expense of others. The weights were used for an uncertainty analysis, applied to the 'critical
690 phosphorus loading levels' calculated by the model. These are the threshold loadings where

691 a shallow lake will switch from the phytoplankton-dominated turbid state to the macrophytes-
692 dominated clear-water state or vice versa. Apart from lake dimensions and loading, the
693 model was most sensitive to zooplankton growth rate, settling rates and maximum growth
694 rates of phytoplankton and macrophytes as process parameters. The results for the best run
695 showed an acceptable agreement between model and data, i.e., that a regression of the
696 predicted on the observed values did not deviate significantly from the 1:1 line, and that
697 nearly all lakes to which the model was applied were classified well as either 'clear'
698 (macrophyte-dominated) or 'turbid' (phytoplankton-dominated). The critical loading levels for
699 a chosen standard lake showed about a factor two uncertainty due to the variation in the
700 posterior parameter distribution (**Janse et al. 2010**). **Janse et al. (2008)** calculated how the
701 critical loading levels depend on water depth, lake size, retention time, proportional marsh
702 area and type of sediment.
703 PCLake has been used in several other case studies, both in static and dynamical
704 way, allowing water managers to evaluate both benefits and drawbacks of proposed
705 restoration measures beforehand.The dynamical case studies, with detailed water and
706 nutrient budgets as input, include: management options for the Reeuwijk Lakes (**Janse et al.**
707 **1993**); different scenarios for water level fluctuations for Lake Oldambt (**Witteveen+Bos**
708 **2009**) and Lake Loenderveen and Terra Nova (**Witteveen+Bos 2010c**); the impact of a
709 sediment trap on water quality in Lake Loosdrecht (**Witteveen+Bos 2008b**), the impact of
710 fish and sediment removal in Bergse Plassen, the impact of different water storage
711 scenarios in Lake Oldambt (**Witteveen+Bos 2009**) and Nieuwe Driemanspolder
712 (**Witteveen+Bos 2010a**), and the impact of water flushing in Wieringen Borderlake
713 (**Witteveen+Bos 2008a**).
714 The static applications of the model imply the estimation of the critical P loading of
715 lakes, i.e. the switchpoints between the (usually undesired) turbid state and the (usually
716 desired) clear-water state. Estimation of the critical loadings of a lake is important for lake
717 managers and is part of the diagnostic framework for shallow lakes recently developed in
718 The Netherlands (**STOWA 2008**). Depending on the difference between actual P loading

719 and critical P loading, measures can be taken to 1) reduce the actual nutrient loading, 2)
720 increase the critical loadings of water systems by adjusting lake characteristics or 3) change
721 the ecological status directly by, for instance, fish removal (**Meijer 2000**). **Janse (2005)** and
722 **Janse et al. (2008)** calculated critical loadings for some 50 European lakes. Critical loadings
723 were calculated for both existing (e.g. Lake Zuidlaren, Lake Breukeleveen) and new water
724 systems (e.g. Eendragtspolder, Nieuwe Driemanspolder) to be used in management
725 projects, giving insight into the robustness of the system to eutrophication. Although PCLake
726 is basically zero-dimensional, it has been run on a grid base. In particular, the design of new
727 water systems (e.g. Wieringen Borderlake, Lake Oldambt) can be optimized by identifying
728 sensitive parts. A combination of a temporal, spatial and static approach was used here.
729 Although it was not intended from the beginning to model climate change effects, the
730 fact that the temperature dependencies of all processes are included, allowed preliminary
731 simulations of the effects of temperature rise, the results being mainly in agreement with
732 observations that warming will decrease the critical loading levels (**Schep et al. 2007**; **Mooij**
733 **et al. 2007**). **Mooij et al. (2009)** showed that the PCLake results were qualitatively
734 comparable with those of a minimal dynamic model.
735
736 ***A metamodel of PCLake***
737 In order to provide water managers with an easy-to-use method to estimate the critical P
738 loading of their lakes, a metamodel of PCLake has been developed. This generates static
739 lake-specific critical P loadings without the need to dynamically run PCLake itself. The first
740 version can be accessed on the Internet (**Janse et al. 2006**); an improved version was
741 published recently by **Witteveen+Bos (2010b)**. Input variables are initial state, water depth,
742 fetch, marsh area, residence time, soil type and background extinction. The range and
743 distribution of each variable were derived from an analysis of Dutch lake characteristics,
744 resulting in a dataset with 41492 different sets of input variables. The critical nutrient
745 loadings is determined much more accurately than previously through 18 iterations,
746 revealing approximately 10^5 possible model outcomes per set of variables between 0 and 10

747 $mg \cdot m^{-2} \cdot d^{-1}$. The factor “Secchi depth / water depth” was used as criterion for the ecological
748 state of the lake (‘clear’ or ‘turbid’), as it was very sensitive for small changes in P-loading
749 around the switch point. The results of all model runs were stored and analysed by different
750 mathematical techniques to derive the metamodel: multiple regression, regression trees,
751 black box neural network and the new technique white box neural network (WBN). Each
752 method was applied separately for three soil types and two initial states, resulting in six
753 different models for each method. The dataset was divided into two parts, in which 83% is
754 used for calibration and 17% for validation. The neural network methods gave the best
755 results; the white box neural network (with an R^2 of 0.96 and a relative error of 0.19) was
756 used for the metamodel because of a better interpretability. In any case, the average relative
757 errors of the neural networks were smaller than the model uncertainty (assuming an average
758 relative error of 0.4 in PCLake). Simplification (pruning) of the neural networks provide only
759 little extra value.
760 A general remark on metamodels is that their results are closely linked to the full-
761 scale model they are derived from, implying the need for recalculating the metamodel in
762 case of future changes in the latter.
763
764 ***Links with other model approaches***
765 Interest from water managers triggered a parallel implementation as a ‘quality module’ in the
766 1-D or 2-D-horizontal water transport model DUFLOW (**STOWA 1999; 2000**). **Fragoso et al.**
767 **(2009)** coupled the model (partly adapted for subtropical lakes) with a 3-D hydrodynamic
768 model. **Prokopkin et al. (2010)** applied relevant parts of PCLake in an existing 1-D-vertical
769 model of the stratified saline Lake Shira. Furthermore, PCLake has been coupled with
770 empirical relations for species richness within functional groups, derived from a multi-lake
771 dataset (**De Meester et al. 2006**). The links with the IPH and Shira models are described
772 here in some more detail.
773
774 ***IPH-TRIM3D-PCLAKE***

IPH-TRIM3D-PCLake model is a complex ecosystem model (available to download at www.peld.ufrgs.br). A detailed description of the model can be found in **Fragoso et al. (2009)**. This model consists of a three-dimensional hydrodynamic module coupled with an ecosystem module. Together the models describe the most important hydrodynamic, biotic, and abiotic components of an aquatic ecosystem. The hydrodynamic model is based on the Navier-Stokes equations, which describe dynamically the three-dimensional transport and mixing of water. An efficient numerical semi-implicit Eulerian-Lagrangian finite difference scheme was used in order to assure stability, convergence, and accuracy (**Casulli and Cheng 1992**; **Casulli and Cattani 1994**). The chemical and biological dynamics in the open water and in the sediment are based on PCLake, with an adaptation to subtropical lakes by including omnivorous fish. The IPH-TRIM3D-PCLake ecosystem model further differs from PCLake, as it takes into account: (a) the horizontal spatial heterogeneity in the aquatic system at the cell level; and (b) stratification over the water column for several state variables (e.g. temperature, water density, nutrients, phytoplankton, and zooplankton). In order to solve the advection-diffusion transport equation for each component in the water numerically, a flux limiting scheme was implemented that uses Roe's superbee limiter (**Roe 1985**) with a second-order Lax-Wendroff scheme (**Hirsch 1990**). Water temperature is modelled through a heat budget algorithm (**Chapra 1997**). The main inputs of the model are: water inflow, infiltration or seepage rate (if any), nutrient loading, particulate loading, temperature, light, wind, rainfall and evaporation, spatial maps (including waterbody bathymetry, bottom and surface stress coefficient, etc.), sediment features, and initial conditions.

One-dimensional vertical model of Lake Shira

A one-dimensional vertical model of Lake Shira (**Prokopkin et al. 2010**) was developed by applying ideas and formulations in PCLake concerning ecosystem dynamics to a relatively rare type of natural waterbody, namely brackish lakes. For these lakes strong stratification of physical-chemical and biological components is typical, together with low species diversity.

These features provide special conditions for ecosystem functioning and nutrient cycling. In this model a one-dimensional algorithm describing the hydrodynamic and thermal structure of Lake Shira has been used **(Belolipetsky et al. 2010)**. As the temperature stratification of Lake Shira is pronounced in summer, it is important to describe this phenomenon correctly and use this effect everywhere in the model. The temperature regime is affected by wind-induced mixing, solar heating and heat exchange with the atmosphere. With regard to ecosystem processes, the impact of temperature was introduced when considered essential and where data were available. Processes such as phyto- and zooplankton growth, respiration, sedimentation, mineralization, etc., use functions mainly derived from PCLake. The resulting patterns of phytoplankton, nutrients and other dynamics show qualitative and quantitative agreement with the field observations during the summer season (**Prokopkin et al. 2010**).

Limitations of PCLake

The main advantage of a complex model like PCLake – its integrated nature – of course also constitutes its main problem: the large number of process parameters, of which the ranges can hardly be assessed all together from one data set. Seen from this perspective, the model analysis carried out by **Janse et al. (2010**) gives only incomplete estimates of parameters. Nevertheless, some parameters can, and have been, reasonably well estimated from experimental data. Some simplifications and/or lumping of process formulations might be a promising direction. On the other hand, some factors are missing, such as the impact of sulphate, iron and nitrate on processes that lead to internal nutrient cycling and eutrophication.

A major limitation in PCLake is the assumption of a uniform water depth, leading to an 'all or nothing' response in lakes, which should show a more gradual response in reality because of depth variations. This limitation can sometimes be overcome by a 'grid setup' (e.g. **Witteveen+Bos 2008a, 2009, 2010a**), but this is not generally applicable and it limits the use of the model for resuspension management measures. A complete 2-D or even 3-D

implementation is possible (see **Fragoso et al. 2009**), but creates, among other problems, excessive computational time. A (pseudo-)1- or 2-D version in the horizontal would, however, increase the applicability. A 2-D implementation in the x-z-plane would allow accounting for the movement of animal populations between different habitats (e.g. **Vos et al. 2002**; **Winder et al. 2004**).

Some management questions ask for a further splitting of some model components in more detailed groups, e.g. macrophytes and/or fish species. Some model experiments have been done in this direction (e.g. **Janse et al. 1995**), such as in the related ditch model PCDitch that includes several groups of macrophytes (**Janse and Van Puijenbroek 1998**; **Janse 2005**). Regarding fish, an oversimplification of the fish module currently appears to produce incorrect results for the effects of biomanipulation. For macrophytes, the potential impact of species like *Elodea* and *Ceratophyllum* on internal eutrophication is underestimated. Finally, results with use of the marsh module are not always consistent with experience, because of oversimplified relations between marsh size and water level. Further weaknesses, following from the model's initial aim and setup, are that it focuses on shallow (non-stratified) lakes, and is restricted to temperate lakes (but see the studies by **Fragoso et al. (2009)**). Not only may some of the parameters be sensitive to changes in climate, but also the structure of the ecosystems may change (see below).

While the model has a closed balance for phosphorus and nitrogen, dynamics of inorganic carbon are not modelled. This limits linkage of PCLake with models that focus on the effect of atmospheric CO_2 elevation on freshwater ecosystems (e.g. **Schippers et al. 2004**).

Regarding the technical aspects, an easy-to-use, freely available user interface, allowing both easy 'hands-on' simulation and visualization for individual lakes, spatial (network) simulations, batch simulations for sensitivity studies and calibration runs, and flexibility in model structure, has not yet been produced. Batch analyses would benefit from a procedure to renew the initial conditions.

Future perspectives for PCLake

There are four types of questions that may influence the future development of PCLake. In the first instance, the applicability for lake managers will be improved by a closer relation with management options (including additional testing) and improvement of the user interface. The planning will be done in cooperation with Dutch water managers, with the limitations mentioned above in mind, and may imply adding detail or, alternatively, making simplifications. The spatial structure of the model (vertically and/or horizontally) will be made adaptable to specific needs. It might be helpful to cooperate with other models for certain aspects.

Secondly, policy makers ask for a lake model that can be used for projections on a global scale, i.e., covering a wider range of lake characteristics, including size and morphology, climate zones and hydrological features, to be embedded in an existing global catchment and land use model for anthropogenic pressures (**PBL 2009**, **Alkemade et al. 2009, in press**). PCLake may be helpful, besides other model approaches, in the set-up of such a model.

Thirdly, the link with biodiversity modelling will be strengthened, which deserves much attention both on global (**MEA 2005**) and regional scales. We refer to the discussion section for possible directions.

Finally, the PCLake model, or specific submodules or cut-outs from it, will be continuously available for use in other projects, such as the application for stratified saline lakes presented in this volume (**Prokopkin et al. 2010**, **Degermendzy et al. 2010**).

Closing remarks on PCLake

The long exposition of PCLake in this paper might suggest that the model and its development did not suffer from the two wasteful trends of model development ('*reinventing the wheel*' and '*having tunnel vision*') that are central to our message. It is not our intention to create this impression. In the Dutch setting PCLake was developed independently from the other major Dutch lake ecosystem model DELFT3D-ECO (and its predecessors).

887 Moreover, in the development of PCLake the focus has always been on food web dynamics,
888 with a more limited attention for spatial dynamics. One the positive side, and as documented
889 above, PCLake has now been embedded in models focussing on spatial dynamics, and has
890 also been linked with minimal dynamic models and static models. The discussion that
891 follows, concerning 'leading principles', might shed some more light on the choices made
892 during the development of PCLake and the other models mentioned in this paper.
893

894 # Discussion

895 ***Leading principles***

896 The rather arbitrarily chosen sample of lake models presented above indeed shows the
897 diversity of approaches to lake ecosystem modelling. Because these approaches differ in
898 many respects, and overlap to various degrees, there is no single axis along which they can
899 be adequately categorized. In an attempt to classify them we scored each approach using
900 multiple criteria concerning model components (Table 1) and model characteristics (Table
901 2). But perhaps the simplest way to get an overview of the whole range of approaches, and
902 an appreciation of their virtues and vices, is to look at the leading principle that led to the
903 development of each approach.

904 Static models are developed from an empirical perspective with no or limited
905 attention given to the underlying mechanisms. With their strong backing by data, they have
906 successfully convinced scientists, water quality managers and politicians from the 1970s
907 onwards that eutrophication had a strong negative impact on aquatic ecosystems, and they
908 still provide useful rules of thumb for water quality management.

909 Another important approach is that of complex dynamic lake ecosystem models
910 based on differential equations. Two leading principles prevail here: a focus on spatial
911 complexity and hydrology in 1, 2 or 3 dimensions and a focus on food web structure and
912 complexity. The fact that in many models one of these two important aspects of aquatic

913 ecosystems is better developed than the other suggests a trade-off between spatial
914 complexity versus food-web complexity in model development.
915 Within the category of complex dynamic models, more detailed knowledge on the
916 leading principles that shaped each particular model could be identified, giving a better
917 understanding of the choices and assumptions that were made during model development.
918 This should enable model developers to (1) better take advantage of the already existing
919 principles and models, thus avoid '*reinventing the wheel*', and also to (2) modify and (3)
920 combine the strengths of these principles and models. We stress, at the same time, the
921 importance of breaking with the undesirable fragmentation in the development of complex,
922 dynamic, lake ecosystem models, which currently exists within the modelling community.
923 While complex ecosystem models were considered very promising in the early
924 1980s, when powerful computers became widely available (**Rigler and Peters 1995**), they
925 were heavily criticised in the 1990s for being data-hungry, overly complex, and not leading to
926 scientific insight or predictive power (for a critical discussion on complex dynamic models
927 see also **Håkanson and Peters (1995)**).
928 Often the underlying model algorithms employ a simple 'engineering-based'
929 paradigm, where small-scale ecosystem processes (e.g., algal growth, bacterial
930 mineralization of nutrients, etc.) are 'scaled-up' (**Flynn, 2005**). For example, fluxes of
931 nutrients between simulated pools are approximated using semi-empirical algorithms
932 determined in laboratory microcosms and applied within lake-scale models with little regard
933 of organism adaptability or more complex ecological interactions (**Arhonditsis and Brett**
934 **2004**). Where attempts are made to resolve the higher ecological interactions such as fish
935 and benthic communities within a spatially-resolved hydrodynamic model, a lack of suitable
936 validation data and excessive model complexity in the absence of guidance by sound
937 empirical data hinders progress and often means that trophic levels above phytoplankton
938 grazers are ignored. Furthermore, while the approach of using a couple hydrodynamic-
939 ecological model can improve our understanding of the physical, chemical and biological
940 roles influencing water quality dynamics, it generally remains unclear whether all important

941 ecosystem feedback mechanisms are represented. These fundamental limitations can have
942 a profound impact on their ability to predict responses to change, and whether 'emergent'
943 ecosystem behaviours (patterns that emerge due to complex system dynamics) such as
944 those observed in nature can be resolved.

945 The above mentioned points of criticism of complex dynamic models stimulated the
946 development of minimal dynamic models. These models build on basis of the seminal work
947 on predator-prey interactions by **Rosenzweig and MacArthur (1963)** and **Rosenzweig**
948 **(1971)** and aim at understanding non-linear processes and alternative stable states in lake
949 ecosystems (and many other dynamic systems) (e.g. **Scheffer 1990**; **Scheffer et al. 1993,**
950 **2001b, 2007**). Even though they are highly abstract and do not produce quantitative output
951 that is of direct use to water quality management, they fully accomplished their goal of
952 generating general insight into large scale mechanisms and had a surprisingly strong impact
953 on management strategies for mitigating anthropogenic stress factors such as
954 eutrophication.

955 The notion that the dynamics of higher trophic levels with their complex life-histories,
956 ontogenetic shifts and behaviour cannot be captured in a single state variable representing
957 their carbon content alone led to the development of individual-based approaches (see
958 **DeAngelis and Mooij 2005**, for a review of individual-based models of ecological and
959 evolutionary processes). As explained in detail above, various 'schools' exist within this
960 broader approach, each with their own leading principles. While models based on super-
961 individuals aim for including empirical realism and detail, physiologically structured and
962 stage-structured biomass models aim for mathematical tractability. Both allow for taking into
963 account the intricate and sometimes non-intuitive effects of ontogenetic development on
964 food web dynamics. Also trait-based models can be qualified as individual-based. Here the
965 focus is on adaptation at various levels of integration, and its consequences for food web
966 dynamics. Again, these models are mostly developed within the constraints set by
967 mathematical tractability.
968

969 ***Challenges and opportunities: Ecological aspects***

970 *Modelling the impact of climate change with eutrophication models*

971 One of the aims with documenting in detail the multi-decadal development of PCLake was to
972 show how a model that was applied to eutrophication studies is now also applied to climate
973 studies. On the positive side, the results obtained so far show that, qualitatively, model
974 output for climate scenarios (**Mooij et al. 2007**) coincides with what we know from empirical
975 studies (**Mooij et al. 2005**) and with general patterns obtained with minimal dynamic models
976 (**Mooij et al. 2009**). Importantly, the impacts of eutrophication and climate change are tightly
977 linked and, therefore, require a model that simultaneously deals with both aspects. On the
978 negative side, however, these predictions have not yet been verified in a formal comparison
979 of model output with the scarce field data that we have on the interplay between
980 eutrophication and climate change (in particular climate warming, e.g. **Moss et al. 2003**; **Van**
981 **der Bund et al. 2004**; **Jeppesen et al. 2009, 2010**). Cross latitude studies that indicate
982 major changes in the trophic structure in lakes may challenge model performance. The
983 composition of fish stocks is expected to change towards higher dominance of
984 zooplanktivorous and omnivorous fish, implying increased predation on zooplankton and,
985 consequently, less grazing on phytoplankton (less top-down control), and a higher
986 chlorophyll:TP ratio (higher yield). Moreover, in warmer lakes fish are smaller, grow faster,
987 mature earlier and have shorter life spans, allocate more energy to reproduction, and have a
988 higher degree of omnivory than populations at higher latitudes, both between and within
989 species (**Blanck and Lammouroux 2007**; **Jeppesen et al. 2010**). While several models
990 include fish dynamically, most of the changes described above are not included, which may
991 lead to too conservative predictions of the effect of climate change. The direction of the
992 cross-latitude changes from cold to warm lakes, that in part might reflect also
993 biogeographical difference and differences in lake age, are largely confirmed in time series
994 from northern temperate lakes (e.g. **Jeppesen et al. 2009, 2010**).

995 In addition, the effects of plants on water clarity seem weaker in subtropical lakes
996 than in north temperate lakes (**Jeppesen et al. 2007**). Hence, **Bachmann et al. (2002)**

found no differences in chlorophyll:TP or Secchi depth:TP relationships in subtropical lakes with low, medium-high or high plant coverage or the amount of plant volume present (% PVI). This suggests that the refuge for zooplankton is poor in warm lakes, which is confirmed by comparative experimental studies conducted in temperate Denmark and subtropical Uruguay (**Meerhoff et al. 2007**). Moreover, a cross-system analysis of data from lakes from the temperate zone to the tropics gave evidence for a lower probability of macrophyte dominance in warm lakes and lower nutrient thresholds for loss of these plants (**Kosten et al. 2009**). No complex models have included such effects, which apparently play an important role for changes in the function of shallow lakes ecosystems and their water clarity as they get warmer, although preliminary PCLake results are in agreement with this direction (**Mooij et al. 2008**).

Another main challenge for predicting effects of climate change is the difficulty in accurately predicting regional wind speed and precipitation (and thus the boundary condition data that feed into the lake ecosystem models). While air temperature predictions from the global climate models are considered relatively reliable from the global climate models, regional wind speed and precipitation (and thus runoff) predictions are still unreliable, and certain variables, such as radiation, are rarely entered as input to the models. However, considerable progress is currently being made in this field **(IPCC 2007; Sipkay et al. 2009)**. Similarly, it is highly uncertain which effects global change will have in the catchment scale, where increasing temperatures, changing land use and frequency of extreme events will lead to changing nutrient fluxes into the surface waters. A study on the influence of altered hydrological regimes brought about by shifting precipitation patterns in eastern Australia using ELCOM-CAEDYM has highlighted the potential significance of this on water quality processes (**Vilhena et al. 2010**).

A final point that we would like to make here is that climate studies have shown that in the temperate zone changing conditions in winter may be as important as, or even more important, than changing conditions in summer. For instance, warm winters may lead to larger inocula of cyanobacteria and higher winter fish survival , leading to blooms and

deteriorated water quality in the following summer. Also many invasive species benefit from warmer winters. In addition, increasing winter temperatures in boreal regions would impact lake surface freezing dynamics. We feel that the issue of 'winter limnology' has not yet gained the attention it needs in the light of climate change.

Both from scientific and policy-oriented sides there is a great need for a lake model able to grasp the impact of combined anthropogenic factors (land use, climate change, fisheries and others) on ecosystem structure and function for a broad range of lake types. The combination of dynamical models with empirical relations might be a fruitful approach.

Modelling biodiversity

A certain level of biodiversity is included in models like Delft-3D Eco, DYRESM-CAEDYM and PCLake, but the level of detail is still far from the biodiversity that we observe in lakes. Several studies have related species richness in natural lakes with global factors such as latitude, altitude, lake size and water chemistry (e.g. **Amarasinghe and Welcomme 2002**) and productivity (e.g. **Leibold 1999**; **Jeppesen et al. 2000**; **Declerck et al. 2007**). Many model applications rather deal with functional diversity by defining, for example, functional phytoplankton groups instead of using single species definitions and, therefore, do not allow projections for species richness. Probably, one of the main obstacles to including more details on biodiversity in models of aquatic ecosystems is that we still lack understanding of the mechanisms maintaining biodiversity. One line of research is to include variations within functional groups and study the effects on ecosystem functioning. Currently, there is an ongoing debate about the role of niche-based versus neutral processes in maintaining biodiversity and potential links between the two theories. Another line of research focuses on deterministic chaos as an explanation for the observed biodiversity and strong fluctuations of the dominant species within functional groups. PROTECH fits in the niche-based approach and seems to indicate that considerable progress can be made along this line. Structurally dynamic and trait-based models also aim at capturing shifts in species composition, though they are still in a pre-mature stage.

An alternative approach is to calculate species diversity, functional diversity and size diversity from empirically based relationships using output variables (e.g. TP) from the complex ecological models. An example is the combination of empirical relations with PCLake output for total P, chlorophyll-a and other variables for a dataset of European lakes (**De Meester et al., 2006**). Another (maybe more policy-or conservation-driven) indicator of biodiversity, as used in the GLOBIO model (**PBL, 2009, Alkemade et al., in press**), is 'biodiversity intactness' (**Scholes and Biggs, 2005**): or the (remaining) mean abundance of the species that are native to the specific type of ecosystem, which has been linked to lake environmental factors such as nutrients (e.g. **Alkemade et al., in press**). Another possible link is to add a functional-ecological index comparable to the 'Depletion Index' or 'Marine Trophic Index' as used in marine Ecosim models.

Modelling of sediment diagenesis, and coupling of diagenetic processes to water column dynamics

It is well known that the amount and availability of nutrient pools in lake sediments can strongly influence the ecological dynamics of the overlying water column (**Søndergaard et al. 2003**), and can even prevent or delay the response of lake water quality to changes in external forcing, such as changes in nutrient loading or climate (**Jeppesen et al. 2005, 2007**). However, sediment nutrient cycling is often not dynamically accounted for, or only included through very simplistic representations, by lake ecosystem models, and it will be a great challenge to improve this element of the models, thus being able to dynamically simulate the response (and resilience) of lake ecosystems to changes in nutrient loading and/or climate, rather than to converge on a new equilibrium state.

Both relatively simple two-layer oxic/anoxic sediment diagenesis models (e.g. **Wang et al. 2003a, b**) and multi-layer, one-dimensional, complex diagenesis models have been available for decades (e.g., **Jørgensen et al. 1982; Boudreau 1996**). Therefore, the most challenging aspect of improving representations of sediment dynamics in lake ecosystem models is not to develop new sediment diagenesis models, but rather to obtain sediment

1081 nutrient data for testing, modification, calibration and validation of already existing models,
1082 as these data are rarely (or never) available at appropriate spatial scales over sufficiently
1083 long time periods (extending one or several decades) (e.g.,**Trolle et al, 2010**).
1084
1085 *Modelling fisheries in an ecosystem context*
1086 There is an increasing trend towards modelling fisheries in an ecosystem context in
1087 both marine (**Hall and Mainprize 2004**) and freshwater systems (**Kitchell et al. 2000**;
1088 **Lammens et al. 2002**). In both systems, studies on the impact of bottom-up processes
1089 through the food web on fisheries have been stimulated by effective management leading to
1090 re-oligotrophication of systems that had become eutrophied. In such cases, it has been
1091 questioned whether minimum levels of carrying capacity of the system for stocks of fish
1092 should be maintained. These stocks can be of interest for a commercial fishery, for sport
1093 fishing, or as food for bird species that have a protected status and hence there is a demand
1094 for embedding fisheries in lake ecosystem models. Ecosystem Based Fishery Management
1095 (EBFM; **EPAP 1999**) is a significant departure from traditional fisheries management. EBFM
1096 considers the impact that fishing has on all aspects of the ecosystem, not just the target
1097 species (**Pikitch et al 2004**). Starting from a different perspective, **Makler-Pick (2010)**, has
1098 demonstrated the utility of linking an individual-based fish population model with a complex
1099 hydrodynamic-food web model (DYRESM-CAEDYM) to explore the impact of fishery
1100 management on the water quality of Lake Kinneret (Israel). The model allows the study of
1101 the role of the fish in a lake ecosystem and has to potential to serve as an EBFM tool, since
1102 it also includes fishery mortality.
1103
1104 ***Challenges and opportunities: Conceptual and technical aspects***
1105 *Model complexity*
1106 We take the point of view that a single 'right' approach or level of complexity does not exist.
1107 Instead, multiple modelling approaches, applied concurrently to a given problem, can help in
1108 developing an integrated view on the functioning of lake ecosystems (**Scheffer 1998, p308**;

Van Nes and Scheffer 2004; **Mooij et al. 2009**). This is a shift in paradigms away from the hopes in the seventies and eighties of the past century that, with increasing computational power, a full reductionist approach to ecosystem dynamics would yield both insight and predictive power. In the new view, we acknowledge that each modelling approach has fundamental shortcomings that cannot be overcome purely through enhanced computational power. To give an example, recent advantages in deterministic chaos as an explanation for the maintenance of planktonic biodiversity (**Huisman and Weissing 1999**) through 'super-saturated coexistence' (**Schippers et al. 2001**) could only have been made using minimal dynamic models. But minimal dynamic models will never to able to provide water quality managers with the input they need in the management of biodiversity.

From this perspective, the recent advance in water-related cyber-infrastructure, defined as the system of hardware and software components that monitor, manage and model aquatic ecosystems (**Shade et al 2009**), has created challenges and opportunities for lake modelling. For example, assimilation of observations from real-time lake sensors to reduce error and uncertainty in model parameterizations is emerging as a promising tool to deal with this issue. For water quality or ecological applications it remains challenging. There are examples, however, where lake metabolism has been computed from real-time oxygen and temperature measurements, and then used to update the parameters of complex hydrodynamic-ecological models used to forecast lake conditions.

Multiple-model paradigm

A more plain approach is to accept all the virtues and shortcomings of each model and respect their identities. This is analogous to approaches and themes taken by the Intergovernmental Panel on Climate Change for their assessment of atmospheric climate models (global circulation models), where, for example, 23 climate models were applied individually, and their simulations for outgoing radiation were collated to produce a range of simulations (**Randall et al. 2007**). It was found that the simple arithmetic mean 'model' of all model simulations, which in itself has no ecological meaning, was the most accurate in

predicting outgoing radiation. Such a multiple-model study will not just provide a quick overview of equally valid model alternatives to potential users or lake managers, but will also give insights into selection of essential model features to a particular problem for the model developers. Whereas its benefits are obvious, adoption of this paradigm into lake ecosystem modelling may of course not be straightforward, as many lakes have highly variable natural conditions and anthropogenic impacts, and different models may have different scopes. Also the recently formed Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES, **Larigauderie and Mooney 2010**) advocates multi-model studies as a basis for future biodiversity assessments. Models for freshwater biodiversity, coupled to global change and other drivers, are urgently needed to support policies at different geographical levels.

Directly linking approaches

In specific cases, however, different approaches can be linked directly. New knowledge can be discovered through tight interactions between data based and deterministic approaches - top-down modelling can validate and inform bottom-up modelling, and vice versa, in a feedback loop, to ultimately result in a more comprehensive understanding of lake response to perturbation. A good example is the derivation of static models from complex dynamic models in so-called ‘metamodels’. As documented above, such a link between dynamic and static applications has been realized for PCLake. In this particular example, the purpose of static applications is to derive a system-dependent critical loading of nutrients. The purpose of dynamic applications is to better understand the relative importance of different characteristics to the ecological functioning of a specific lake, through which key factors can be identified, and to make specific predictions of the impact of management measures on ecological functioning.

Other possibilities for a direct link between modelling approaches are the inclusion of physiologically structured or stage-structured modules for fish and zooplankton in complex ecosystem models.This usefulness of making this link was recently shown in the DYCS-

FISH model for simulating fish populations in aquatic systems (**Makler-Pick 2010**) that was mentioned earlier.

Calibration, uncertainty and error-propagation

While the topics of model calibration, uncertainty and error propagation are of overwhelming importance in many of the more complex modelling approaches, we will be brief here, especially in the light of the many publications on this topic (see citations in **Arhonditsis and Brett 2004; Arhonditsis et al. 2007**; **Janse et al. 2010**). In view of our discussion on complex versus more simple models, the common notion is that a disadvantage of complex models is that they are both difficult to calibrate and 'data hungry'. In this respect it is important to notice that the importance of a clear separation between parameters that are chosen a priori versus those chosen a posteriori. In a study on error propagation in spatially explicit individual-based models **Mooij and DeAngelis (1999, 2003)** showed that in a strict statistical sense complex models of which only a few parameters are estimated a posteriori (calibrated) have even narrower log-likelihood profiles for the estimated parameters than simple models with an equal number of parameters. This gives rise to the counterintuitive notion that complex, more realistic models of which only a few parameters are calibrated may be less 'data hungry' than their simpler counterparts. Further, the procedure of determining sensitivity and uncertainty in complex models, if designed appropriately, can in fact be used to help extract important information about key processes (**Makler-Pick in press**).

Using optimization principles

There has been quite some controversy whether it is acceptable to employ some form of optimization principle in ecological lake models. A widely applied phytoplankton model that employs such principle is BLOOM II (**Los, 2009**). The model is based upon a competition principle for individual ecotypes, which is translated into an equivalent optimization principle at the community level. First the different possible states at which one of the nutrients or light

limits growth of one of the ecotypes are defined. Subsequently the general linear programming algorithm selects from those states, the one at which the potential growth rate of all ecotypes is maximal and the requirement for the resources is minimal. It can be shown analytically that this method effectively gives equal weight to a high potential growth capacity as well as to a low requirements for nutrients and light in determining the algal composition of the system in steady state. To prevent unrealistically fast jumps towards such steady state solutions when BLOOM is embedded in a dynamic model, the realized growth rate of each species is limited to that which is feasible, given temperature and light conditions. Similarly, the model imposes a limit on mortality, to prevent unrealistically rapid declines.

Optimization is also at the heart of the approach of Structurally Dynamic Models (**Håkanson and Peters 1995; Zhang et al 2010**). From a neo-Darwinian point of view, optimizing principles, such as maximization of exergy in SDMs, could be questioned, because these principles act at a high integration level and it is not always obvious how to link these principles with individual fitness. An opportunistic argument in favour of optimisation would be that in practice these models do better in their confrontation with data than models that lack such optimization. Whether this argument remains intact when major changes in environmental pressures occur (e.g. climate change) needs to be tested.

Reusing existing code in other or new models

The core of the majority of models mentioned in this manuscript consists of differential equations. Insofar as these are ordinary differential equations, it is very simple to keep the algorithms in which they are coded separate from other model code. The only slight complication arises when the model contains (nested) if-then-else blocks, resulting in multiple definitions of the same variable (at different conditions), While this facilitates the readability of the model code, it may diffuse the set of equations for a given variable and hamper the reusability of code in some other programming languages. From a perspective of reusability of code the use on conditional statements that combine all assignments for given variable in one line of code might be preferred.

For models built on ordinary differential equations many standard and reliable integration routines are available (e.g. **Press et al. 1992**). However, note that complex dynamic models often contain processes that can have very different time scales. The models may hence be rather stiff, which makes integration not a trivial task. If in addition the ODEs contain discontinuities (if-then statements) standard methods may rather easily generate numerical artifacts that are not obvious.

Insofar as partial differential equations relate to spatial grids, different mathematical integration routines are available, each with their advantages and disadvantages. Moreover, the complexity of these routines usually transcends the mathematical knowledge and skills of ecological modellers and demands involvement of mathematicians. While partial differential equations also are at the heart of physiologically structured models, they demand completely different implementations. Public well-documented libraries for implementing such models are now available (**De Roos 2010**; **Soetaert et al. 2010**). Such libraries facilitate the reusability of model code and such an approach should be encouraged.

Individual-based models are often not well founded in mathematical theory and in particular, deal with time in a very informal way. By this we mean that there is no clear separation between the state of the system at a given moment in time, and the processes that work on these states. This carries the risk that the order in which the model formulations are evaluated has an unknown impact on model outcome. A more formal embedding in mathematics should be possible because most individual-based models are in fact a very complicated set of difference equations (i.e. they consist of long lists of stepwise changes in model states). The most complicated code structure of IBMs in practice prohibits the reuse of code. Recent progress in formalizing the IBM approach has been made, however (**Grimm et al. 2006**).

The model experimentalist

Comparing different model approaches in a systematic and scientific way constitutes an almost unachievable task, as usually more than a single difference exist between two

models. It is therefore difficult to attribute emerging differences in model behavior to specific differences in the model structures. However, the standard methodology of an experimental ecologist is to never change more than one factor at the same time, and the same philosophical principal should hold true for complex models. More scientific insight can be gained when several, competing approaches for specific processes/submodels (e.g. photosynthesis-light model, complexity of higher trophic levels) are implemented in the same model. Then the user can evaluate these submodels systematically while keeping the remaining model conserved and investigate their effects on the model performance.

Use of object oriented programming

Object oriented programming (OOP) is increasingly used in many major software development projects and some OOP frameworks can be useful in facilitating modular model design and reusability of code. Yet, its use in lake ecosystem modelling is still limited.

The 1D hydrodynamic model DYRESM has also been written following OOP principles, although care has to be taken for selecting an appropriate object structure for 2 or 3D hydrodynamic models because of the computationally demanding nature of the numerical solutions. Moreover, PCLake has been implemented in the object-oriented framework OSIRIS (**Mooij and Boersma 1996**), this implementation still does not take full advantage of the potential of this object-oriented framework.

In contrast to modelling the structure of an ecosystem, Petzoldt and Rinke (2007) proposed a rather general object-oriented model using a state-space formulation of a dynamic system. Here the OOP interface represents the model together with its data while preserving full freedom for the core functions. The approach was designed for a convenient implementation of minimal dynamic models in the R language (R Development Core Team 2009), and it allows to establish direct communication between model and solver codes written in compiled languages (**Soetaert et al, 2010**) to avoid communication overhead. Another development worth mentioning here is the work of **Recknagel et al (2008) and Cao et al (2008)**.

The use of OOP within ecosystem modelling codes will ultimately support the portability and wider application of them with physical models of different dimensionality. As exemplified within this paper, depending on site geography and the scientific basis for the modelling study, a number of hydrodynamic solvers are relevant even though the underlying biogeochemical and ecological parameterisations are common. Standards for model coupling and communication (e.g., OpenMI, www.openmi.org) and OOP code standards will allow transferability of model components to a wider range of applications.

Integrating individual-based models with models based on differential equations

It is now widely acknowledged that individual variation and behaviour cannot be ignored when looking in detail at higher trophic levels (**DeAngelis and Mooij 2005**). Fish populations are highly size-structured, while birds often perform seasonal migration. These aspects are easily incorporated in individual-based models. While there are no major technical obstacles that prohibit the integration of physiologically structured models of fish in complex ecosystem models, we are not aware of successful attempts to do so yet. Such developments would also be desirable for zooplankton, where size-structured interactions are known to be critically important for the dynamics of the system (**Hülsmann et al. in press**).

For models based on super-individuals, the situation is conceptually more complex because, as outlined above, these employ a fundamentally different mathematical approach, which is less suitable for integration in models that are based on unsteady differential equations and focus on the conservation of mass. The Lake Kinneret example by **Makler-Pick (2010)** however does suggest that this approach is possible and can be further developed where field data is available. Another example is found in modelling approaches that link individual-based models of fish larvae with nutrient-phytoplankton-zooplankton chains (e.g. **Hermann et al. 2001**).

Model documentation and copyrights on source code

We take the point of view that for the progress of science it is essential that the source code in which the mathematical formulations of the model are turned into a working model is free of copyrights and fully documented to the level where the model can be re-implemented on the basis of the documentation, of course accompanied by a proper citation. We can understand some level of copyright protection, for example, related to the shell in which the model runs and the user-interface through which it is operated; however, full openness in the code will ultimately allow scientists to interrogate the nuances of the numerical algorithms adopted to solve the standard ODE/PDE model equations. This openness serves two purposes. First, it allows for a completely transparent and ongoing evaluation of the correctness of the model. Second, and more importantly, it allows for an easy reimplementation of parts of the model into new models, and this will ultimately facilitate more rapid advance in model developments and associated applications. These new models can be of the same type, or of hybrid types (e.g. a complex dynamic model with a physiologically/stage structured fish or zooplankton module). Openness of source code thus can provide essential technical support to avoid both '*reinventing the wheel*' and '*having tunnel vision*'.

Challenges and opportunities: Recommendations

We would like to finish this paper with a list of practical and hopefully unpresumptuous recommendations that – we believe – may be of help in the further development of lake ecosystem models.

General

- While acknowledging ongoing initiatives like the Register of Ecological Models (REM, www.ecobas.org, Benz et al. 2001), we feel that there is a need for more common venues for the lake ecosystem modelling community (e.g. workshops, conferences and/or a community website), to generate exposure to the scientific world, policy makers, water quality managers and funding agencies, to enhance awareness of

models and model approaches and to transcend individual differences that keep us apart.

- Once a model and its results have been published and can be properly cited, the code describing the process formulations should not be protected by copyrights and should be easily accessible in order to allow easier exchange and integration of different models, to facilitate comparison of different model approaches for the same problem and to allow for an ongoing assessment of the validity of the models.
- Improved availability of global and regional data sets and better collaboration between data collectors and data users are needed to warrant a correct interpretation of the data for further model development and validation.

Ecological

- The importance of top down control by fish and as a determinant of the state of aquatic ecosystems is greater than it is generally assumed and there is a need to incorporate these impacts in lake ecosystem models.
- When incorporating fish, but also with respect to zooplankton, attempts should be made, when observation data allow this, to represent them in a size- or stage-structured manner since size-structured interactions may be fundamental to the dynamics of the system.
- The process of sediment diagenesis as a determinant of the state of aquatic ecosystems is generally overly simplified or neglected altogether, and there is a need to improve this aspect of lake ecosystem models.
- There is an urgent need to focus more on biodiversity in lake ecosystem models. One of the ways to achieve this is by linking empirically based relationships to output from the dynamic models, such as total phosphorous and chlorophyll a.

Conceptual and technical

- Reuse of eutrophication models for studying climate change is a logical step but should be done with great care, because the validity of the outcomes has generally not yet been properly tested against empirical data and field studies show clear synergistic effects that are not well covered by existing models.
- Ongoing change in natural systems demands the inclusion of adaptive processes in lake ecosystem models.
- There is an urgent need to find ways to integrate models focussing on spatial dynamics, hydrology and lower trophic levels with models that focus on the whole food web.
- Sensitivity analysis, calibration and uncertainty analysis is not a one-time exercise but should rather be an ongoing effort within a modelling program.
- During model calibration and validation we should focus not only on state variables, but also on process rates.
- Metamodels provide a powerful tool to bridge the gap between state of the art dynamic models and easy to use static models.
- In general, we believe that it will be fruitful to combine current dynamic and static model approaches.
- In addition to detailed analyses, it is important to study the general non-linear behaviour of complex models using high level input and output parameters (e.g. P-loading, Chlorophyll a concentration).
- IBM approaches to lake ecosystems should give more attention to a proper handling of time and mass balances.
- We promote the modularity of source code through object-oriented programming (OOP) on an adequate level while preserving efficiency, readability and portability of the code.

Concluding remarks

In this paper, we identify two challenges for making further progress in lake ecosystem modelling: to avoid in future work '*reinventing the wheel*' and '*having tunnel vision*'. While

this may sound trivial, and has been stated before, the continuing repetition in published models and the fragmentation of the field of lake ecosystem modelling as a whole brings us to restating them and stressing their importance as we did in this paper. We do not think that the main solution is in technically linking all kinds of models. Instead, we believe that applying multiple modelling approaches concurrently, using existing models and model components, can help to develop an integrated scientific view on the functioning of lake ecosystems and to provide managers with essential ecological information for water quality management.

Acknowledgements

WMM, RG, IP, SG, PV and AD were supported by grant 047.017.012 of the Netherlands Organization for Scientific Research (NWO) and the Russian Foundation for Basic Research (RFBR). LDSD was supported by NWO grant 817.01.007. DT and EJ were supported by EU-REFRESH, EU-WISER, CLEAR (a Villum Kann Rasmussen Centre of Excellence Project on lake restoration) and CRES. We thank Prof. André De Roos for his insight full comments and Dr. Tom Andersen for his contribution to the text. JJ wishes to thank Drs. T. Aldenberg, Dr. L. Van Liere, Mr. M.J. ‘t Hart, Ir. M.H.J.L Jeuken, Ing. S. van Tol, Ir. J.S. Sloot and many others, including the many people who provided lake data, for their contributions to PCLake. This is publication #### of the Netherlands Institute of Ecology (NIOO-KNAW).

References

Abrams PA and Matsuda H (1997) Fitness minimization and dynamic instability as a consequence of predator-prey coevolution. Evolutionary Ecology 11:1-20

Aegis (2001) ACSL Reference manual, v. 1.1; ACSL/MATH User manual, v. 2.5; ACSL/MATH Reference manual, v. 2.5; ACSL/MATH Installation guide, v. 2.5.

Aldenberg T, Janse JH, Kramer PRG (1995) Fitting the dynamic model PCLake to a multi-lake survey through Bayesian Statistics. Ecological Modelling 78:83-99

Alkemade R, Van Oorschot M, Miles L, Nellemann C, Bakkenes M, Ten Brink B (2009) GLOBIO3: A framework to investigate options for reducing global terrestrial biodiversity loss. Ecosystems 12:374-390.

1416 Alkemade R, Janse JH, Van Rooij W, Trisurat Y (in press) Applying GLOBIO at different
1417 geographical levels. In: Y Trisurat, RP Shrestha and R Alkemade (eds), Global Land
1418 Use, Climate change and biodiversity modeling: perspectives and applications. IGI
1419 Allen JI, Eknes M, Evensen G (2003) An Ensemble Kalman Filter with a complex marine
1420 ecosystem model: hindcasting phytoplankton in the Cretan Sea. Annales
1421 Geophysicae 21:399-411
1422 Amarasinghe US, Welcomme RL (2002) An analysis of fish species richness in natural
1423 lakes. Environmental Biology of Fishes 65:327-339
1424 Arhonditsis GB, Brett, MT (2004) Evaluation of the current state of mechanistic aquatic
1425 biogeochemical modeling. Marine Ecology Progress Series 271:13-26
1426 Arhonditsis GB, Qian SS, Stow CA, Lamon EC, Reckhow KH (2007) Eutrophication risk
1427 assessment using Bayesian calibration of process-based models: Application to a
1428 mesotropic lake. Ecological Modelling 208: 215-229
1429 Bachmann RW, Jones BL, Fox DD, Hoyer M, Bull LA, Canfield DE (1996) Relationship
1430 between trophic state indicators and fish biomass in Florida (U.S.A.) lakes. Canadian
1431 Journal of Fisheries and Aquatic Sciences 42:239-249
1432 Bachmann RW, Horsburgh CA, Hoyer MV, Mataraza LK, Canfield DE (2002) Relations
1433 between trophic state indicators and plant biomass in Florida lakes. Hydrobiologia
1434 470:219-234
1435 Baird ME, Suthers IM (2007), A size-resolved pelagic ecosystem model. Ecological
1436 Modelling 203:185-203
1437 Baumert HZ, Benndorf J, Bigalke K, Goldmann D, Nöhren I, Petzoldt Y, Post J, Rolinski S
1438 (2005) Das hydrophysikalisch ökologische Talsperren- und Seenmodel SALMO-HR -
1439 Modelldokumentation und Leitfaden für den Anwender. Dresden,
1440 www.baufachinformation.de/literatur.jsp?bu=2007029013557
1441 Belolipetsky PV, Belolipetskii VM, Genova SN Mooij WM (2010) Numerical modelling of
1442 vertical stratification of Shira Lake in summer. Aquatic Ecology:this Issue
1443 Benndorf J (1995) Possibilities and limits for controlling eutrophication by biomanipulation.
1444 Internationale Revue der gesamten Hydrobiologie 80:519-534
1445 Benndorf J and Recknagel F (1982) Problems of application of the ecological model SALMO
1446 to lakes and reservoirs having various trophic states. Ecological Modelling 17:129-
1447 145
1448 Benz J, Hoch R, Legovic T (2001) ECOBAS - modelling and documentation. Ecological
1449 Modelling 138:3-15
1450 Berger C and Wells S (2008) Modeling the Effects of Macrophytes on Hydrodynamics.
1451 Journal of Environmental Engineering 134:778-788

1452 Blanck A, Lammouroux N (2007) Large-scale intraspecific variation in life-history traits of 44
1453 European freshwater fish. Journal of Biogeography 34:862-875
1454 Blauw AN, Los FJ, Huisman J, Peperzak L (2010). Nuisance foam events and Phaeocystis
1455 globosa blooms in Dutch coastal waters analyzed with fuzzy logic. Journal of Marine
1456 Systems:doi:10.1016/j.jmarsys.2010.05.003
1457 Boudreau BP (1996) A method-of-lines code for carbon and nutrient diagenesis in aquatic
1458 sediments. Computers and Geosciences 22:479-496
1459 Bowen JD, Hieronymous JW (2003) A CE-QUAL-W2 Model of Neuse Estuary for Total
1460 Maximum Daily Load Development. Journal of Water Resources Planning and
1461 Management 129: 283-294
1462 Bruce LC, Hamilton D, Imberger J, Gal G, Gophen M, Zohary T, Hambright KD (2006) A
1463 numerical simulation of the role of zooplankton in C, N and P cycling in Lake
1464 Kinneret, Israel. Ecological Modelling 193:412-436
1465 Burger DF, Hamilton DP, Pilditch C (2007) Modelling the relative importance of internal and
1466 external nutrient loads on water column nutrient concentrations and phytoplankton
1467 biomass in a shallow polymictic lake. Ecological Modelling 211:411-423
1468 Canfield DE, Bachmann RW (1981) Prediction of total phosphorus concentrations,
1469 chlorophyll-a, and Secchi depths in natural and artificial lakes. Canadian Journal of
1470 Fisheries and Aquatic Sciences 38:414-423
1471 Cao HQ, Recknagel F, Joo GJ, Kim DK (2006) Discovery of predictive rule sets for
1472 chlorophyll-a dynamics in the Nakdong River (Korea) by means of the hybrid
1473 evolutionary algorithm HEA. Ecological Informatics 1:43-53
1474 Cao HQ, Recknagel F, Cetin L, Zhang BR (2008) Process-based simulation library SALMO-
1475 OO for lake ecosystems. Part 2: Multi-objective parameter optimization by
1476 evolutionary algorithms. Ecological Informatics 3:181-190
1477 Carpenter SR, Ludwig D, Brock WA (1999) Management of eutrophication for lakes subject
1478 to potentially irreversible change. Ecological Applications 9:751-771
1479 Casulli V, Cattani E (1994) Stability, Accuracy and Efficiency of a Semiimplicit Method for 3-
1480 Dimensional Shallow-Water Flow. Computers & Mathematics with Applications 27:
1481 99-112
1482 Casulli V, Cheng RT (1992) Semiimplicit Finite-Difference Methods for 3-Dimensional
1483 Shallow-Water Flow. International Journal Numerical Methods Fluids 15: 629-648
1484 Chambers PA, Kalff J (1985) Depth distribution and biomass of submersed aquatic
1485 macrophyte communities in relation to Secchi depth. Canadian Journal of Fisheries
1486 and Aquatic Sciences 42:701-709

1487 Chan WS, Recknagel F, Cao HQ, Park HD (2007) Elucidation and short-term forecasting of
1488 microcystin concentrations in Lake Suwa (Japan) by means of artificial neural
1489 networks and evolutionary algorithms. Water Research 41:2247-2255
1490 Chapra SC (1975) Comment on “An empirical method of estimating the the retention of
1491 phosphorus in lakes” by W.B. Kirchner and P.J. Dillon. Water Resources Research
1492 11:1033-1034
1493 Chapra SC (1997) Surface water-quality modeling. McGraw-Hill Series in Water Resources
1494 and Environmental Engineering. 844 pp.
1495 Chapra SC, Reckhow KH (1983) Engineering approaches for lake management. Vol. 2,
1496 Mechanistic modeling. Butterworth Publishers
1497 Christensen V, Pauly D (1993) Trophic models of aquatic ecosystems. ICLARM Conf. Proc.,
1498 Int. Center for Living Resources Management, Manila
1499 Chung SW, Oh JK (2006) Calibration of CE-QUAL-W2 for a monomictic reservoir in a
1500 monsoon climate area. Water Science Technology 54:29-37
1501 Chung SW, Hipsey MR, Imberger J (2009) Modelling the propagation of turbid density
1502 inflows into a stratified lake: Daecheong Reservoir, Korea. Environmental Modelling
1503 and Software 24:1467-1482
1504 Claessen D, De Roos AM, Persson L (2000) Dwarfs and giants: Cannibalism and
1505 competition in size-structured populations. American Naturalist 155:219-237
1506 Cole TM and Wells SA (2008) CE-QUAL-W2: A two-dimensional, laterally averaged,
1507 Hydrodynamic and Water Quality Model, Version 3.6," Department of Civil and
1508 Environmental Engineering, Portland State University, Portland, OR.
1509 De Meester L, Declerck S, Janse JH, Dagevos JJ, Portielje R, Lammens EHRR, Jeppesen
1510 E, Lauridsen T, Schwenk K, Muylaert K, Van Der Gucht K, Vyverman W, Zwart G,
1511 Van Hannen E, Van Puijenbroek PJTM, Conde-Porcuna JM, Sánchez-Castillo P,
1512 Vandekerkhove J, Brendonck L (2006). Biodiversity in European shallow lakes: a
1513 multilevel - multifactorial field study. In: R Bobbink, JTA Verhoeven (eds.), Wetlands
1514 as a natural resource, Vol. 2. Wetlands: functioning, biodiversity conservation and
1515 restoration. Springer-Verlag Berlin Heidelberg. Ecological Studies 191:149-167
1516 De Roos (2010) EBT software. http://staff.science.uva.nl/~aroos/EBTsoftware.htm
1517 De Roos AM, Persson L (2001) Physiologically structured models - from versatile technique
1518 to ecological theory. Oikos 94:51-71
1519 De Roos AM, McCauley E, Wilson WG. (1991) Mobility versus density-limited predatorprey
1520 dynamics on different spatial scales. Proceedings of the Royal. Society. London
1521 Series. B 246:117–22

1522 De Roos AM, Metz JAJ, Diekmann 0 (1992) Studying the dynamics of structured population
1523 models: a versatile technique and its application to Daphnia. American Naturalist
1524 139:123-147
1525 De Roos AM, Schellekens T, Van Kooten T, Van De Wolfshaar K, Claessen D, Persson L
1526 (2008) Simplifying a physiologically structured population model to a stage-structured
1527 biomass model. Theoretical Population Biology 73:47-62
1528 De Senerpont Domis LN, Mooij WM, Hülsmann S, Van Nes EH, Scheffer M (2007) Can
1529 overwintering vs diapausing strategy in Daphnia determine match-mismatch events
1530 in zooplankton-algae interactions. Oecologia 150:682-698
1531 DeAngelis DL, Mooij WM (2005) Individual-based models of ecological and evolutionary
1532 processes. Annual Reviews in Ecology, Evolution and Systematics 36:147-168
1533 Debele B, Srinivasan R. and Parlange J-Y (2006) Coupling upland watershed and
1534 downstream waterbody hydrodynamic and water quality models (SWAT and CE-
1535 QUAL-W2) for better water resources management in complex river basins,
1536 Environmental Modeling and Assessment 13:135-153
1537 Declerck S, Vanderstukken M, Pals A, Muylaert K, De Meester L (2007) Plankton
1538 biodiversity along a gradient of productivity and its mediation by macrophytes.
1539 Ecology 88:2199-2210
1540 Degermendzhi AG, Zadereev ES, Rogozin DYu, Prokopkin IG, Barkhatov YuV, Tolomeyev
1541 AP, Khromechek EB, Mooij WM, Janse JH, Gulati RD (2010) Vertical stratification of
1542 physical, chemical and biological components in two saline lakes Shira and Shunet,
1543 (South Siberia, Russia). Aquatic Ecology:this Issue
1544 Deliman PN, Gerald JA (2002) Application of the Two-Dimensional Hydrothermal and Water
1545 Quality Model, CE-QUAL-W2, to the Chesapeake Bay - Conowingo Reservoir. Lake
1546 and Reservoir Management 18:10-19
1547 Dillon PJ, Rigler FH (1974) The phosphorus-chlorophyll relationships in lakes. Limnology
1548 and Oceanography 19:767-773
1549 Downing JA, Plante C, Lalonde S (1990) Fish production correlated with primary production,
1550 not the mophoedaphic index. Canadian Journal of Fisheries and Aquatic Sciences
1551 47:1929-1936
1552 Downing JA, Watson SB, McCauley E (2001) Predicting cyanobacteria dominance in lakes.
1553 Canadian Journal of Fisheries and Aquatic Sciences 58:1905-1908
1554 Drenner RW, Hambright KD (1999) Review: Biomanipulation of fish assemblages as a lake
1555 restoration technique. Archive für Hydrobiologie 146:129-165
1556 Elliott JA, Irish AE, Reynolds CS (2010) Modelling phytoplankton dynamics in fresh waters:
1557 affirmation of the PROTECH approach to simulation. Freshwater Reviews 3:75-96

1558 EPAP, Ecosystem Principles Advisory Panel (1999) Ecosystem Based Fishery
1559 Management. NOAA National Marine Fisheries Service, Silver Spring, MD.
1560 http://www.nmfs.noaa.gov/sfa/EPAPrpt.pdf
1561 Fitz HC, DeBellevue EB, Costanza R, Boumans R, Maxwell T, Wainger L, Sklar FH (1996)
1562 Development of a general ecosystem model for a range of scales and ecosystems.
1563 Ecological Modelling 88:263-295
1564 Flynn KJ (2005) Castles built on sand: dysfunctionality in plankton models and the
1565 inadequacy of dialogue between biologists and modellers. Journal of Plankton
1566 Research 27:1205-1210
1567 Forbes SA (1887) The lake as a microcosm. Bull. Sci. Assoc., Peoria, Illinois, pp 77-87.
1568 Reprinted in Illinois Natural History Survey Bulletin 15:537-550
1569 Fragoso Jr CR, Van Nes EH, Janse JH, Da Motta Marques D (2009) IPH-TRIM3D-PCLake:
1570 A three-dimensional complex dynamic model for subtropical aquatic ecosystems.
1571 Environmental Modelling and Software 24:1347-1348
1572 Gal G, Hipsey MR, Parparov A, Wagner U, Makler V, Zohary T (2009) Implementation of
1573 ecological modelling as an effective management and investigation tool: Lake
1574 Kinneret as a case study. Ecological Modelling 220:1697-1718
1575 Genova SN, Belolipetskii VM, Rogozin DY, Degermendzhy AG, Mooij WM (2010) A one-
1576 dimensional model of vertical stratification of Lake Shira focussed on winter
1577 conditions and ice cover. Aquatic Ecology:this Issue
1578 Grimm V (1994) Mathematical models and understanding in ecology. Ecological Modelling
1579 75/76: 641-651
1580 Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, Thulke J-H, Weiner J,
1581 Wiegand T, DeAngelis DL (2005) Pattern-oriented modelling of agent-based complex
1582 systems: lessons from ecology. Science 310:987-991
1583 Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T,
1584 Heinz S, Huse G, Huth A, Jepsen JU, Jørgensen C, Mooij WM, Müller B, Robbins
1585 AM, Robbins MM, Rossmanith E, Rüger N, Pe'er G, Piou C, Railsback SF, Strand E,
1586 Souissi S, Stillmann R, Vabø R, Visser U, DeAngelis DL (2006) The ODD/PSPC+3
1587 protocol for describing individual-based and agent-based models. Ecological
1588 Modelling 198:115-126
1589 Gulati RD, Van Donk E (2002) Lakes in the Netherlands, their origin, eutrophication and
1590 restoration: state-of-the-art review. Hydrobiologia 478:73-106
1591 Gulati RD, Lammens EHHR, Meijer M-L, Van Donk E (1990) Biomanipulation, tool for water
1592 management. Hydrobiologia 200/201:1-628

1593 Gulati, RD, Siewersten K, Van Liere L (1991) Carbon and phosphorus relationship of
1594 zooplankton and its seston food in Loosdrecht lakes. Memorie dell'Istituto Italiano di
1595 Idrobiologia 48:279-298
1596 Gunderson LH (2000) Ecological resilience - in theory and application. Annual Review of
1597 Ecology and Systematics 31:425-439
1598 Håkanson L (2000) Modelling radiocesium in lakes and coastal areas - new approaches for
1599 ecosystem modellers. A textbook with Internet support. - Kluwer Academic
1600 Publishers, Dordrecht. 215 pp.
1601 Håkanson L (2006) Suspended particulate matter in lakes, rivers and marine systems. The
1602 Blackburn Press, New Jersey. 331 pp.
1603 Håkanson L and Boulion V (2002) The Lake Foodweb - modelling predation and
1604 abiotic/biotic interactions. Backhuys Publishers, Leiden. 344 pp.
1605 Håkanson L and Peters RH (1995) Predictive limnology - methods for predictive modelling.
1606 SPB Academic Publishers, Amsterdam. 464 pp.
1607 Håkanson L, Bryhn AC,.Hytteborn JK (2007). On the issue of limiting nutrient and predictions
1608 of cyanobacteria in aquatic systems. Science of the Total Environment 379:89-108
1609 Hall SJ, Mainprize B (2004) Towards ecosystem-based fisheries management. Fish and
1610 Fisheries 5:1-20
1611 Hamilton DP (1999) Numerical modelling and lake management: Applications of the
1612 DYRESM model. In: Theoretical Reservoir Ecology and its Applications, JG Tundisi
1613 and M Straskraba (Eds.), pp. 153-174. Backhuys Publ., The Netherlands.
1614 Hamilton DP, Mitchell SF (1996) An empirical model for sediment resuspension in shallow
1615 lakes. Hydrobiologia 317:209-220
1616 Hamilton DP Mitchell SF (1997) Wave-induced shear stresses, plant nutrients and
1617 chlorophyll in seven shallow lakes. Freshwater Biology 38:159-168
1618 Hanson JM, Leggett WC (1982) Empirical prediction of fish biomass and weight. Canadian
1619 Journal of Fisheries and Aquatic Sciences 39:257-263
1620 Hanson JM, Peters RH (1984) Empirical prediction of crustacean zooplankton biomass and
1621 profundal macrobenthos biomass in lakes. Canadian Journal of Fisheries and
1622 Aquatic Sciences 41:439-445
1623 Hansson L-A, Annadotter H, Bergman E, Hamrin SF, Jeppesen E, Kairesalo T, Luokkanen
1624 E, Nilsson P-Å, Søndergaard M, Strand J (1998) Biomanipulation as an application of
1625 food-chain theory: constraints, synthesis, and recommendations for temperate lakes.
1626 Ecosystems 1:558-574
1627 Hardy FJ, Shortreed KS, Stockner JG (1986) Bacterioplankton, phytoplankton and
1628 zooplankton communities in a British Clolumbia Coastal lake before and after nutrient
1629 reduction. Canadian Journal of Fisheries and Aquatic Sciences 43:1504-1514

1630 Harper D (1992) Eutrophication of Freshwaters: principles, problems and restoration.
1631 Chapman & Hall, London
1632 Harris GP (2006) Pattern, process and prediction in aquatic ecology – a limnological view of
1633 some general ecological problems. Freshwater Biology 32:143-160
1634 Hermann AJ, Hinckley S, Megrey BA and Napp JM (2001) Applied and theoretical
1635 considerations for constructing spatially explicit individual-based models of marine
1636 larval fish that include multiple trophic levels. ICES Journal of Marine Science
1637 58:1030-1041
1638
1639 Hipsey MR, Hamilton DP (2008) Computational Aquatic Ecosystem Dynamic Model:
1640 CAEDYM v3 Science Manual. Centre for Water Research Report, University of
1641 Western Australia
1642 Hipsey MR, Antenucci JP, Brookes JD (2008) A generic, process-based model of microbial
1643 pollution in aquatic systems, Water Resources Research, 44:W07408, 26pp.
1644 Hirsch C (1990) Numerical Computation of Internal and External Flows, Volume 2:
1645 Computational Methods for Inviscid and Viscous flows, 1st Ed., Wiley, Chichester,
1646 England
1647 Hoyer MV, Canfield DE (1994) Bird abundance and species richness on Florida lakes:
1648 influence of trophic status, lake morphology, and aquatic macrophytes. Hydrobiologia
1649 279/280:107-119
1650 Huisman J, Weissing FJ (1999) Biodiversity of plankton by species oscillations and chaos.
1651 Nature 402:407-410
1652 Hülsmann S, Rinke K, Mooij WM (2005) A quantitative test of the size efficiency hypothesis
1653 by means of a physiologically structured model. Oikos 100:43-54
1654 Hülsmann S, Rinke K, Mooij WM (in press) Size-selective predation and predator-induced
1655 life history shifts alter the outcome of competition between planktonic grazers.
1656 Functional Ecology doi: 10.1111/j.1365-2435.2010.01768.x
1657 Huston M, DeAngelis D, Post W. 1988. New computer models unify ecological theory.
1658 BioScience 38:682-691
1659 Ibelings BW, Vonk M, Los FJ, Van Der Molen DT, Mooij WM (2003) Fuzzy modeling of
1660 cyanobacterial surface waterblooms, validation with 12 years of NOAA-AVHRR
1661 satellite images. Ecological Applications 13:1456-1472
1662 IPCC (2007) Climate Change 2007: Impacts, Adaptation and Vulnerability. ML Parry et al.
1663 (eds) Contribution of Working Group II to the Fourth Assessment Report of the
1664 Intergovernmental Panel on Climate Change. Cambridge University Press,
1665 Cambridge

Janse JH, Van der Does J, Van der Vlugt JC (1993) PCLake: Modelling eutrophication and its control measures in Reeuwijk Lakes. In: G Giussani and C Callieri (eds.), Proceedings 5th International Conference on the Conservation and Management of Lakes, Stresa (Italy):117-120

Janse JH (1997) A model of nutrient dynamics in shallow lakes in relation to multiple stable states. Hydrobiologia 342:1-8

Janse JH (2005) Model studies on the eutrophication of shallow lakes and ditches, Wageningen University, Wageningen. (available at http://edepot.wur.nl/121663)

Janse JH, Van Liere L (1995) PCLake - a modeling tool for the evaluation of lake restoration scenarios. Water Science Technology 31:371-374

Janse JH, Van Puijenbroek PJTM (1998) Effects of eutrophication in drainage ditches. Environmental Pollution 102, S1:547-552

Janse JH, Aldenberg T, Kramer PRG (1992) A mathematical-model of the phosphorus cycle in Lake Loosdrecht and simulation of additional measures. Hydrobiologia 233:119-136

Janse JH, Van Donk E, Gulati RD (1995) Modelling nutrient cycles in relation to food-web structure in a biomanipulated shallow lake. Netherlands Journal of Aquatic Ecology 29:67-79

Janse JH, Ligtvoet W, Van Tol S, Bresser AHM (2001) A model study on the role of wetland zones in lake eutrophication and restoration. TheScientificWorldJournal [electronic resource] 1 Supplement 2:605-614

Janse JH, Schep S, Klinge M, Witmer MCH (2006) Metamodel PCLake, http://www.pbl.nl/nl/dossiers/water/modellen/WerkingModelPCLake.html

Janse JH, De Senerpont Domis LN, Scheffer M, Lijklema L, Van Liere L, Klinge M, Mooij WM (2008) Critical phosphorous loading of different types of shallow lakes and the consequences for management estimated with the ecosystem model PCLake. Limnologica 38:203-219

Janse JH, Scheffer M, Lijklema L, Van Liere L, Sloot JS, Mooij WM (2010) Estimating the critical phosphorus loading of shallow lakes with the ecosystem model PCLake: Sensitivity, calibration and uncertainty. Ecological Modelling 221:654-665

Jeppesen E, Jensen JP, Søndergaard M, Lauridsen TL, Pedersen LJ, Jensen L (1997) Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia 342/343:151-164

Jeppesen E, Søndergaard M, Christoffersen K. eds. (1998) The structuring role of submerged macrophytes in lakes. Springer Verlag

1701 Jeppesen E, Jensen JP, Sondergaard M, Lauridsen T, Landkildehus F (2000). Trophic
1702 structure, species richness and biodiversity in Danish lakes: Changes along a
1703 phosphorus gradient. Freshwater Biology 45:201-218.
1704 Jeppesen E, Sondergaard M, Jensen JP (2003) Climatic warming and regime shifts in lake
1705 food webs – some comments. Limnology and Oceanography 48:1346–1349
1706 Jeppesen E, Søndergaard M, Jensen JP, Havens K, Anneville O, Carvalho L, Coveney MF,
1707 Deneke R, Dokulil M, Foy B, Gerdeaux D, Hampton SE, Kangur K, Köhler J, Körner
1708 S, Lammens EHRR, Lauridsen TL, Manca M, Miracle R, Moss B, Nõges P, Persson
1709 G, Phillips G, Portielje R, Romo S, Schelske CL, Straile D, Tatrai I, Willén E, Winder
1710 M (2005) Lake responses to reduced nutrient loading- an analysis of contemporary
1711 long-term data from 35 case studies. Freshwater Biology 50:1747-1771
1712 Jeppesen E, Meerhoff M, Jacobsen BA, Hansen RS, Søndergaard M, Jensen JP, Lauridsen,
1713 TL, Mazzeo N, Branco CW (2007) Restoration of shallow lakes by nutrient control
1714 and biomanipulation - the successful strategy varies with lake size and climate.
1715 Hydrobiologia 581:269-285
1716 Jeppesen E, Kronvang B, Meerhoff M, Søndergaard M, Hansen KM, Andersen HE,
1717 Lauridsen TL, Beklioglu M, Ozen A, Olesen JE (2009) Climate change effects on
1718 runoff, catchment phosphorus loading and lake ecological state, and potential
1719 adaptations. Journal of Environmental Quality 38:1930-1941
1720 Jeppesen E, Meerhoff M, Holmgren K, González-Bergonzoni I, Teixeira-De Mello F,
1721 Declerck SAJ, De Meester L, Søndergaard M, Lauridsen TL, Bjerring R, Conde-
1722 Porcuna JM, Mazzeo N, Iglesias C, Reizenstein M, Malmquist HJ, Balayla D (2010)
1723 Impacts of climate warming on lake fish community structure and dynamics, and
1724 potential ecosystem effects. Hydrobiologia 646:73-90
1725 Jones JR, Bachmann RW (1976) Prediction of phosphorus and chlorophyll levels in lakes.
1726 Journal Water Pollution Control Federation 48:2176-2182
1727 Jørgensen SE (1995) State-of-the-art of ecological modelling in limnology. Ecological
1728 Modelling 78:101-115
1729 Jørgensen SE (1999) State-of-the-art of ecological modelling with emphasis on development
1730 of structural dynamic models. Ecological Modelling 120:75-96
1731 Jørgensen SE (2008) Overview of the model types available for development of ecological
1732 models. Ecological Modelling 215:3-9
1733 Jørgensen SE (2010) A review of recent developments in lake modelling. Ecological
1734 Modelling 221:689-692
1735 Jørgensen SE, Bendoricchio G (2001) Fundamentals of ecological modelling, 3rd ed.
1736 Elsevier

1737 Jørgensen SE, Kamp-Nielsen L and Mejer HF (1982) Comparison of a simple and a
1738 complex sediment phosphorus model. Ecological Modelling 16:99-124
1739 Jørgensen SE, Halling-Sørensen B, Nielsen SN (1995) Handbook of environmental and
1740 ecological modeling. CRS Lewis Publishers, Boca Raton
1741 Kankaala P, Huotari J, Peltomaa E, Saloranta T and Ojala A (2006) Methanotrophic activity
1742 in relation to methane efflux and total heterotrophic bacterial production in a stratified,
1743 humic, boreal lake. Limnology and Oceanography 51:1195-1204
1744 Kirchner WB, Dillon PJ (1975) An empirical method of estimating the the retention of
1745 phosphorus in lakes. Water Resources Research 11:182-183
1746 Kitchell JF, Cox SP, Harvey CJ, Johnson TB, Mason DM, Schoen KK, Aydin K, Bronte C,
1747 Ebener M, Hansen M, Hoff M, Schram S, Schreiner D, Walters CJ (2000)
1748 Sustainability of the Lake Superior fish community: Interactions in a food web
1749 context. Ecosystems 3:545-560
1750 Kohavi R. (1995) A study of cross-validation and bootstrap for accuracy estimation and
1751 model selection. In: Proceedings of the Fourteenth International Joint Conference on
1752 Artificial Intelligence. Morgan Kaufmann, San Mateo, California:1137-1143
1753 Kooijman SALM (2000) Dynamic energy and mass budgets in biological systems (2nd
1754 edition). Cambridge University Press
1755 Kosten S, Kamarainen A, Jeppesen E, Van Nes EH, Peeters ETHM, Mazzeo N, Hauxwell J,
1756 Hansel-Welch N, Lauridsen TL, Søndergaard M, Bachmann RW, Lacerot G, Scheffer
1757 M (2009) Likelihood of abundant submerged vegetation growth in shallow lakes
1758 differs across climate zones. Global Change Biology 15:2503-2517
1759 Kuo, J-T, Lung W-S, Yang C-P, Liu W-C, Yang M-D and Tang T-S. (2006) Eutrophication
1760 modelling of reservoirs in Taiwan. Environmental Modelling and Software 21:829-844
1761 Kuo J-T, Liu W-C, Lin R-T, Lung W-S, Yang M-D, Yang C-P, Chu S-C (2007) Water quality
1762 modeling for the Feitsui reservoir in northern Taiwan. Journal of the American Water
1763 Resources Association 39:671-687
1764 Kuznetsov YA (1995) Elements of Applied Bifurcation Theory. Springer-Verlag, New York.
1765 591 pp.
1766 Laanemets J, Lilover MJ, Raudsepp U, Autio R, Vahtera E, Lips I, Lips U (2006). A Fuzzy
1767 Logic Model to Describe the Cyanobacteria Nodularia spumigena Blooms in the Gulf
1768 of Finland, Baltic Sea. Hydrobiologia 554:31-45
1769 Lammens EHRR, Van Nes EH, Mooij WM (2002) Differences in exploitation of the bream
1770 population in three Dutch lakes and their relation to water quality. Freshwater Biology
1771 47:2435-2442

1772 Larigauderie A, Mooney HA (2010) The Intergovernmental science-policy Platform on
1773 Biodiversity and Ecosystem Services: moving a step closer to an IPCC-like
1774 mechanism for biodiversity. Current opinion in Environmental Sustainability 2:9-14
1775 Larsen DP, Mercier HT (1976) Phosphorus retention capacity of lakes. Journal of the
1776 Fisheries Research Board of Canada 33:1742-1750
1777 Leibold MA (1999). Biodiversity and nutrient enrichment in pond plankton communities.
1778 Evolutionary Ecology Research 1:73-95
1779 Leon LF, Smith REH, Hipsey MR, Bocaniov SN, Higgins SN, Hecky RE, Antenucci JP,
1780 Guildford SJ (in press) Application of a 3D hydrodynamic-biological model for
1781 seasonal and spatial dynamics of water quality and phytoplankton in Lake Erie.
1782 Journal of Great Lakes Research
1783 Leppäranta M (1993) A review of analytical models of sea-ice growth. Atmosphere-Ocean
1784 31:123-138
1785 Levins R (1966) The strategy of model building in population biology. American Scientist
1786 54:421-431
1787 Lewis DM, Brookes JD, Lambert MF (2004) Numerical models for management of Anabaena
1788 circinalis. Journal of Applied Phycology 16:457-468
1789 Li YK, Song B, Chen Y, Chen LQ, Yu N, Olson D (2010) Changes in the trophic interactions
1790 and the community structure of Lake Taihu (China) ecosystem from the 1960s to
1791 1990s. Aquatic Ecology 44:337-348
1792 Litchman E, Klausmeier C, Schofield O, Falkowski P (2007) The role of functional traits and
1793 trade-offs in structuring phytoplankton communities: scaling from cellular to
1794 ecosystem level. Ecology Letters 10:1170-1181
1795 Los FJ (2009) Eco-hydrodynamic modelling of primary production in coastal waters and
1796 lakes using BLOOM. Wageningen University, Wageningen. (available at
1797 http://edepot.wur.nl/1249)
1798 Lydersen E, Aanes KJ, Andersen S, Andersen T, Brettum P, Bækken T, Lien L, Lindstrøm
1799 EA, Løvik JE, Mjelde M, Oredalen TJ, Lyche AS, Ropmstad R, Rørslett B, Saloranta
1800 T (2003) THERMOS-projektet: Fagrapport 1998-2002. NIVA rapport 4720-2003.
1801 Norwegian Institute for Water Research, Oslo, Norway 119pp. (in Norwegian)
1802 MacKay, MD, Neale PJ, Arp CD, De Senerpont Domis LN, Fang X, Gal G, Jöhnk K, Kirillin
1803 G, Lenters JD, Litchman E, MacIntyre S, Marsh P, Melack J, Mooij WM, Peeters F,
1804 Quesada A, Schladow SG, Schmid M, Spence C, Stefan HG, Stokes SL (2009)
1805 Modelling lakes and reservoirs in the climate system. Limnology and Oceanography
1806 54:2315-2329

1807 Makler-Pick V (2010) A computer ecosystem model applied to studying the food web and
1808 water quality of Lake Kinneret, with emphasis on topdown control. PhD thesis,
1809 Faculty of Civil and Environmental Engineering, Technion, Haifa, Israel
1810 Makler-Pick V, Gal G, Gorfine M, Hipsey MR, Carmel Y (in press) Sensitivity analysis for
1811 complex ecological models - a new approach. Environmental Modelling and Software
1812 Mao, J.Q., Lee JHW (2009). The extended Kalman filter for forecast of algal bloom
1813 dynamics. Water Research 43:4214-4224
1814 MEA (2005) Inland Water Systems. In: Millennium Ecosystem Assessment, Ecosystems and
1815 Human Well-being: Current State and Trends, Volume 1, Chapter 20:551-584
1816 Meerhoff MM, Clemente FTM, Iglesias C, Pedersen AR, Jeppesen E (2007) Can warm
1817 climate-related structure of littoral predator assemblages 26 weaken the clear water
1818 state in shallow lakes? Global Change Biology 13:1888-1897
1819 Meijer ML (2000) Biomanipulation in the Netherlands: 15 years of experience. Thesis,
1820 Landbouwuniversiteit Wageningen, Wageningen
1821 Merico A, Bruggeman J, Wirtz KW (2009) A trait-based approach for downscaling complexity
1822 in plankton ecosystem models. Ecological Modelling 220:3001-3010
1823 Metz JAJ, Diekmann 0 (1986) The dynamics of physiologically structured populations.
1824 Springer-Verlag
1825 Mooij WM (1996) Variation in abundance and survival of larval fish in shallow eutrophic lake
1826 Tjeukemeer. Environmental Biology of Fishes 46:265-279
1827 Mooij WM, Boersma M (1996) An object-oriented simulation framework for individual-based
1828 simulations (OSIRIS): Daphnia population dynamics as an example. Ecological
1829 Modelling 93:139-153
1830 Mooij WM, DeAngelis DL (1999) Error propagation in spatially explicit population models: a
1831 reassessment. Conservation Biology 13:930-933
1832 Mooij WM, DeAngelis DL (2003) Uncertainty in spatially explicit animal dispersal models.
1833 Ecological Applications 13:794-805
1834 Mooij WM, Hülsmann S, Vijverberg J, Veen A, Lammens EHRR (2003) Modeling Daphnia
1835 population dynamics and demography under natural conditions. Hydrobiologia
1836 491:19-34
1837 Mooij WM, Hülsmann S, De Senerpont Domis LN, Nolet BA, Bodelier PLE, Boers PCM,
1838 Pires, LMD, Gons HJ, Ibelings BW, Noordhuis R (2005) The impact of climate
1839 change on lakes in the Netherlands: a review. Aquatic Ecology 39:381-400
1840 Mooij WM, Janse JH, De Senerpont Domis LN, Hülsmann S, Ibelings BW (2007) Predicting
1841 the effect of climate change on temperate shallow lakes with the ecosystem model
1842 PCLake. Hydrobiologia 584:443-454

1843 Mooij WM, De Senerpont Domis LN, Hülsmann S (2008) The impact of climate warming on
1844 water temperature, timing of hatching and young-of-the-year growth of fish in shallow
1845 lakes in the Netherlands. Journal of Sea Research 60:32-43
1846 Mooij WM De Senerpont Domis LN, Janse JH (2009) Linking species- and ecosystem-level
1847 impacts of climate change in lakes with a complex and a minimal model. Ecological
1848 Modeling 220:3011-3020
1849 Moss B, Mckee D, Atkinson D, Collings SE, Eaton JW, Gill AB, Harvey I, Hatton K, Heyes T,
1850 Wilson D (2003) How important is climate? Effects of warming, nutrient addition and
1851 fish on phytoplankton in shallow lake microcosms. Journal of Applied Ecology
1852 40:782-792
1853 Norberg J (2004) Biodiversity and ecosystem functioning: a complex adaptive systems
1854 approach. Limnology and Oceanography 49:1269-1277
1855 Ostfeld A. and Salomons S (2005) A hybrid genetic-instance based learning algorithm for
1856 CE-QUAL-W2 calibration. Journal of Hydrology 310:122-142
1857 PBL (2009). GLOBIO-aquatic, http://www.globio.info
1858 Petzoldt T, Rinke K (2007) Simecol: An Object-Oriented Framework for Ecological Modeling
1859 in R. Journal of Statistical Software 22(9): 1-31
1860 Petzoldt T, Uhlmann D (2006) Nitrogen emissions into freshwater ecosystems: Is there a
1861 need for nitrate elimination in all wastewater treatment plants? Acta Hydrochimica et
1862 Hydrobiologica 34:305-324
1863 Petzoldt T, Rolinski S, Rinke K, König M, Baumert HZ, Benndorf J (2005): SALMO: Die
1864 ökologische Komponente des gekoppelten Modells. Wasserwirtschaft 95:28-33 (in
1865 German)
1866 Pikitch EK, Santora C, Babcock EA, Bakun A, Bonfil R, Conover DO, Dayton P, Doukakis P,
1867 Fluharty D, Herman B, Houde ED, Link J, Livingston PA, Mangel M, McAllister MK,
1868 Pope J, Sainsbury KJ (2004) Ecosystem based fishery management. Science
1869 305:346-347
1870 Press WH, Teukolsky SA, Vetterling WT, Flannery BP (1992) Numerical Recipes in C: The
1871 Art of Scientific Computing, 2nd Ed. Cambridge University Press. Cambridge. 994
1872 pp.
1873 Prokopkin IG, Mooij WM, Janse JH, Degermendzhy AG (2010) A general one-dimensional
1874 vertical ecosystem model of Lake Shira (Russia, Khakasia): description,
1875 parametrization and analysis. Aquatic Ecology:this Issue
1876 R Development Core Team (2009) R: A language and environment for statistical computing.
1877 R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL
1878 http://www.R-project.org.

1879 Randall RG, Kelso JRM, Minns CK (1995) Fish production in freshwaters: are rivers more
1880 productive than lakes? Canadian Journal of Fisheries and Aquatic Sciences 52:631-
1881 643
1882 Randall DA, Wood RA, Bony S, Colman R, Fichefet T, Fyfe J, Kattsov V, Pitman A, Shukla
1883 J, Srinivasan J, Stouffer RJ, Sumi A, Taylor KE (2007) Cilmate Models and Their
1884 Evaluation. In: Climate Change 2007: The Physical Science Basis. Contribution of
1885 Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on
1886 Climate Change, S Solomon, D Qin, M Manning, Z Chen, M Marquis, KB Averyt,
1887 MTignor, HL Miller (eds.), Cambridge University Press, Cambridge, United Kingdom
1888 and New York, NY, USA
1889 Reckhow KH (1979) Empirical lake models for phosphorus: development, applications,
1890 uncertainty. In: D Scavia, A Robertson (eds.), Perspectives on Lake Ecosystem
1891 Modelling. Ann Arbor Science, Ann Arbor:193-222
1892 Reckhow KH, Chapra SC (1983) Data Analysis and Empirical Modeling. Butterworth
1893 Publishers, Boston. 340 pp.
1894 Recknagel F, Cao H, Kim B, Takamura N, Welk A (2006) Unravelling and forecasting algal
1895 population dynamics in two lakes different in morphometry and eutrophication by
1896 neural and evolutionary computation. Ecological Informatics 1:133-151
1897 Recknagel F, Cetin L, Zhang BR (2008) Process-based simulation library SALMO-OO for
1898 lake ecosystems. Part 1: Object-oriented implementation and validation. Ecological
1899 Informatics 3:170-180
1900 Reichert P, Mieleitner J (2008) Lake Models. In: Jørgensen SE and Fath BD (Eds.),
1901 Ecological Models. Vol. 3 of Encyclopedia of Ecology, 2068-2080. Oxford: Elsevier
1902 Revenga C, Campbell I, Abell R, De Villiers P, Bryer M (2005) Prospects for monitoring
1903 freshwater ecosystems towards the 2010 targets. Philosophical Transactions of the
1904 Royal Society B Biological Sciences 360:397-413
1905 Reynolds CS, Irish AE, Elliott JA (2001) The ecological basis for simulating phytoplankton
1906 responses to environmental change (PROTECH). Ecological Modelling 140:271-291
1907 Rigler FH, Peters RH (1995) Science and limnology. Excellence in ecology no. 6. xxvi,
1908 Ecology Institute Oldendorf/Luhe, Germany. 239pp.
1909 Riley MJ, Stefan HG (1988) MINLAKE: a dynamic lake water quality simulation model.
1910 Ecological Modelling 43:155-182
1911 Rinke K, Hülsmann S, Mooij WM (2008) Energetic costs, underlying resource allocation
1912 patterns and adaptive value of predator-induced life-history shifts. Oikos 117:273-285
1913 Robson, B.J. and Hamilton, D.P. 2003: Three-dimensional modelling of a Microcystis bloom
1914 event in the Swan River estuary. Ecological Modelling 174:203-222

1915 Robson BJ, Hamilton DP, Webster IT, Chan T (2008) Ten steps applied to development and
1916 evaluation of process-based biogeochemical models of estuaries. Environmental
1917 Modelling and Software 23:369-384
1918 Roe PL (1985) Some contributions to the modelling of discontinuous flows. Lectures in
1919 Applied Mathematics 22:163-193
1920 Roland F, Lobão L, Vidal LO, Jeppesen E, Paranhos R, Huszar VM (2010) Relationships
1921 between pelagic bacteria and phytoplankton abundances in contrasting tropical
1922 freshwaters. Microbial Ecology 60:261-272
1923 Rolinski S, Petzoldt T, Baumert HZ, Bigalke K, Horn H, Benndorf J (2005): Das physikalisch-
1924 ökologisch gekoppelte Talsperrenmodell. Wasserwirtschaft 95:34-38 (in German)
1925 Rosenzweig ML (1971) Paradox of enrichment: destabilization of exploitation ecosystems in
1926 ecological time. Science 171:385-387
1927 Rosenzweig ML, MacArthur RH (1963) Graphical representation and stability conditions of
1928 predator prey interactions. American Naturalist 97:209-223
1929 Saito L, Johnson BM, Bartholow J, Hanna RB (2001) Assessing Ecosystem Effects of
1930 Reservoir Operations Using Food Web-Energy Transfer and Water Quality Models.
1931 Ecosystems 4:105-125
1932 Sakamoto M (1966) Primary production by the phytoplankton community in some Japanese
1933 lakes and its dependence upon lake depth. Archive für Hydrobiologie 62:1-28
1934 Salonen K, Leppäranta M, Viljanen M, Gulati RD (2009) Perspectives in winter limnology:
1935 closing the annual cycle of freezing lakes. Aquatic Ecology 43:609-616
1936 Saloranta TM (2000) Modeling the evolution of snow, snow ice and ice in the Baltic Sea.
1937 Tellus 52A:93-108
1938 Saloranta TM (2006) Highlighting the model code sselection and application process in
1939 policy-relevant water quality modelling. Ecological Modelling 194:316-327
1940 Saloranta TM, Andersen T (2007) MyLake—A multi-year lake simulation model code
1941 suitable for uncertainty and sensitivity analysis simulations. Ecological Modelling
1942 207:45-60
1943 Saloranta TM, Forsius M, Järvinen M, Arvola L (2009) Impacts of projected climate change
1944 on the thermodynamics of a shallow and deep lake in Finland: model simulations and
1945 Bayesian uncertainty analysis. Hydrology Research 40:234-248
1946 Salski A, Holsten B (2006) A fuzzy and neuro-fuzzy approach to modelling cattle grazing on
1947 pastures with low stocking rates in Middle Europe. Ecological Informatics 1:269-276.
1948 Savage VM, Webb CT and Norberg J (2007) A general multi-trait-based framework for
1949 studying the effects of biodiversity on ecosystem functioning. Journal of Theoretical
1950 Biology 247:213-229

1951 Schauser I, Strube T (2007) Perspectives of lake modelling towards predicting reaction to
1952 trophic change. Kompetenzzentrum Wasser Berlin Publication Series, volume 9
1953 Scheffer M (1990) Multiplicity of stable states in fresh water systems. Hydrobiologia 200:475-
1954 486
1955 Scheffer M, (1998) Ecology of shallow lakes. Chapman & Hall, London. 357 pp.
1956 Scheffer M, Beets J (1994) Ecological models and the pitfalls of causality. Hydrobiologia
1957 276:115-124
1958 Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E (1993) Alternative equilibria in
1959 shallow lakes. Trends in Ecology and Evolution 8:275-279
1960 Scheffer M, Baveco JM, DeAngelis DL, Rose KA, Van Nes EH (1995) Super-individuals a
1961 simple solution for modelling large populations on an individual basis. Ecological
1962 Modelling 80:161-170
1963 Scheffer M, Rinaldi S, Kuznetsov YA, Van Nes EH (1997) Seasonal dynamics of Daphnia
1964 and algae explained as a periodically forced predator-prey system. Oikos 80:519-532
1965 Scheffer M, Straile D, Van Nes EH, Hosper H (2001) Climatic warming causes regime shifts
1966 in lake food webs. Limnology and Oceanography 46:1780-1783
1967 Scheffer M, Carpenter S, Foley JS, Folke C, Walker B (2001) Catastrophics shifts in
1968 ecosystems. Nature 413:591-596
1969 Scheffer M, Van Nes EH (2007) Shallow lakes theory revisited: various alternative regimes
1970 driven by climate, nutrients, depth and lake size. Hydrobiologia 584:455-466
1971 Schep SA, Ter Heerdt, GNJ, Janse JH, Ouboter M (2007) Possible effects of climate change
1972 on ecological functioning of shallow lakes, Lake Loenderveen as a case study.
1973 Annals of Warsaw University of Life Sciences - SGGW. Land Reclamation. Volume
1974 38, Volume 38 / 2007
1975 Schippers P, Verschoor AM, Vos M, Mooij WM (2001) Does “supersaturated coexistence”
1976 resolve the “paradox of the plankton”? Ecology Letters 4:404-407
1977 Schippers P, Vermaat JE, De Klein J, Mooij WM (2004) The effect of atmospheric CO2
1978 elevation on plant growth in freshwater ecosystems. Ecosystems 7:63-74
1979 Scholes RJ, Biggs R (2005). A biodiversity intactness index. Nature 434:45-49
1980 Shade A, Carey CC, Kara E, Bertilsson S, McMahon KD, Smith MC (2009) Can the black
1981 box be cracked? The augmentation of microbial ecology by high-resolution,
1982 automated sensing technologies. The ISME Journal 3:881-888
1983 Sipkay Cs, Kiss KT, Vadadi-Fülöp Cs, Hufnagel L. (2009) Trends in research on the possible
1984 effects of climate change concerning aquatic ecosystems with special emphasis on
1985 the modelling approach. Applied Ecology and Environmental research 7:171-198
1986 Soetaert K, Petzoldt T, Setzer RW (2010) Solving differential equations in R: package
1987 deSolve. Journal of Statistical Software 33:1-25

1988 Sollie S, Janse JH, Mooij WM, Coops H, Verhoeven JTA (2008) The contribution of the
1989 marsh zones to water quality in Dutch shallow lakes: a modelling study.
1990 Environmental Management 42:1002-1016
1991 Sommer U, Gliwicz ZM, Lampert W, Duncan A (1986) The PEG-model of seasonal
1992 succession of planktonic events in fresh waters. Archive für Hydrobiologie 106:433-
1993 471
1994 Søndergaard M, Liboriussen L, Pedersen AR, Jeppesen E (2008) Lake restoration by fish
1995 removal: Short and Long-term effects in 36 Danish lakes. Ecosystems 11:1291-1305
1996 Søndergaard M, Jensen JP and Jeppesen E (2003) Role of sediment and internal loading of
1997 phosphorus in shallow lakes. Hydrobiologia 506:135-145
1998 Søndergaard M, Johansson LS, Lauridsen TL, Jørgensen TB, Liboriussen L, Jeppesen E
1999 (2010) Submerged macrophytes as indicators of the ecological quality of lakes.
2000 Freshwater Biology 55:893-908
2001 Spence DHN (1982) The Zonation of plants in fresh-water lakes. Advances in Ecological
2002 Research 12:37-125
2003 STOWA (1999) Procesbeschrijvingen DUFLOW, versie 3. (Process models in DUFLOW,
2004 version 3.) STOWA, Utrecht, report nr. 99-21 (In Dutch)
2005 STOWA (2000) DUFLOW for Windows v.3.3; User's Guide, Reference Guide. STOWA,
2006 Utrecht, report no. 2000-27
2007 STOWA (2008) Van helder naar troebel ... en weer terug (From clear to turbid ... and back
2008 again), STOWA, Utrecht. Report 2008-04 (In Dutch)
2009 Sullivan BA, Jager HI, Myers R (2003) Modeling white sturgeon movement in a reservoir: the
2010 effect of water quality and sturgeon density. Ecological Modelling 167:97-114
2011 Tian R C 2006 Toward standard parameterizations in marine biological modeling. Ecological
2012 Modelling 193:363-386
2013 Tirok K and Gaedke U (2010) Internally driven alternation of functional traits in a multi-
2014 species predator-prey system. Ecology 91:1748-1762
2015 Trolle D, Skovgaard H, Jeppesen E (2008a) The Water Framework Directive: Setting the
2016 phosphorus loading target for a deep lake in Denmark using the 1D lake ecosystem
2017 model DYRESM-CAEDYM. Ecological Modelling 219:138-152
2018 Trolle D, Jørgensen TB, Jeppesen E (2008b) Predicting the effects of reduced external
2019 nitrogen loading on the nitrogen dynamics and ecological state of deep Lake Ravn,
2020 Denmark, using the DYRESM-CAEDYM model. Limnologica 38:220-232
2021 Trolle T, Hamilton DP, Pilditch CA (2010) Evaluating the influence of lake morphology,
2022 trophic status and diagenesis on geochemical profiles in lake sediments. Applied
2023 Geochemistry 25: 621–632

2024 Van De Bund WJ, Romo S, Villena MJ, Valentin M, Van Donk E, Vicente E, Vakkilainen K,
2025 Svensson M, Stephen D, Stahl-Delbanco A, Rueda J, Moss B, Miracle MR, Kairesalo
2026 T, Hansson LA, Hietala J, Gyllstrom M, Goma J, Garcia P, Fernandez-Alaez M,
2027 Fernandez-Alaez C, Ferriol C, Collings SE, Becares E, Balayla DM, Alfonso T (2004)
2028 Responses of phytoplankton to fish predation and nutrient loading in shallow lakes: a
2029 pan-European mesocosm experiment. Freshwater Biology 49:1608-1618
2030 Van Donk E, Santamaria L, Mooij WM (2003) Climate warming causes regime shifts in lake
2031 food webs: a reassessment. Limnology and Oceanography 48:1350-1353
2032 Van Liere L, Janse JH (1992) Restoration and resilience to recovery of the Lake Loosdrecht
2033 ecosystem in relation to its phosphorus flow. Hydrobiologia 233:95-104
2034 Van Nes EH, Scheffer M (2004) A strategy to improve the contribution of complex simulation
2035 models to ecological theory. Ecological Modelling 185:153-164
2036 Van Nes EH, Lammens EHRR and Scheffer M (2002) PISCATOR, an individual-based
2037 model to analyze the dynamics of lake fish communities. Ecological Modelling
2038 152:261-278
2039 Van Nes EH, Scheffer M, Van den Berg MS, Coops H (2003) Charisma: a spatial explicit
2040 simulation model of submerged macrophytes. Ecological Modelling 159:103-116
2041 Vilhena LC, Hillmer I., Imberger J (2010) The role of climate change in the occurrence of
2042 algal blooms; Lake Burragorang, Australia. Limnology and Oceanography 55:1188-
2043 1200
2044 Vollenweider RA (1968) Scientific fundamentals of the eutrophication of lakes and flowing
2045 waters, with particular reference to nitrogen and phosphorus as factors in
2046 eutrophication. OECD, Paris. Tech. Rpt. DA 5/SCI/68.27. 250 pp.
2047 Vollenweider RA (1975) Input-output models with special reference to the phosphorus
2048 loading concept. Schweizerische Zeitschrift für Hydrologie 37:53-84
2049 Vollenweider RA, Kerekes J (1982) Eutrophication of waters. Monitoring, assessment and
2050 control. OECD Cooperative programme on monitoring of inland waters
2051 (Eutrophication control), Environment Directorate, OECD, Paris. 154 pp.
2052 Vos M, Flik BJG, Vijverberg J, Ringelberg J, Mooij WM (2002) From inducible defences to
2053 population dynamics: modelling refuge use and life-history changes in Daphnia.
2054 Oikos 99:386-396
2055 Vos M, Kooi BW, Mooij WM, DeAngelis DL (2004) Inducible defenses and the paradox of
2056 enrichment. Oikos 105:471-480
2057 Wallace BB, Hamilton DP (2000) Simulation of water-bloom formation in the cyanobacterium
2058 Microcystis aeruginosa, Journal of Plankton Research 22: 1127-1138
2059 Wang H, Appan A and Gulliver JS (2003a) Modeling of phosphorus dynamics in aquatic
2060 sediments: I - model development. Water Research 37:3928-3938

Wang H, Appan A and Gulliver JS (2003b) Modeling of phosphorus dynamics in aquatic sediments: II - examination of model performance. Water Research 37, 3939-3953.

Winder M, Spaak P, Mooij WM (2004) Trade-offs in zooplankton habitat selection. Ecology 85:2027-2036

Wirtz KW and Eckhardt B (1996) Effective variables in ecosystem models with an application to phytoplankton succession. Ecological Modelling 92:33-53

Witteveen+Bos (2008a) Nadere uitwerking waterkwaliteit en ecologische kwaliteit Wieringerrandmeer. rapport nr. WRW5-32 (In Dutch)

Witteveen+Bos (2008b) Watersysteemanalyse Loosdrechtse Plassen. rapport nr. LOOS20-1-1 (In Dutch)

Witteveen+Bos (2009) Effecten peilbeheer en waterberging Oldambtmeer. rapport nr. VDM53-1-1 (In Dutch)

Witteveen+Bos (2010a) Waterkwaliteit herinrichting Nieuwe Driemanspolder. rapport nr. ZTM99-1-1 (In Dutch)

Witteveen+Bos (2010b) Neuraal netwerk PCLake ten behoeve van KRW-verkenner. rapport nr. UT565-2-1 (In Dutch)

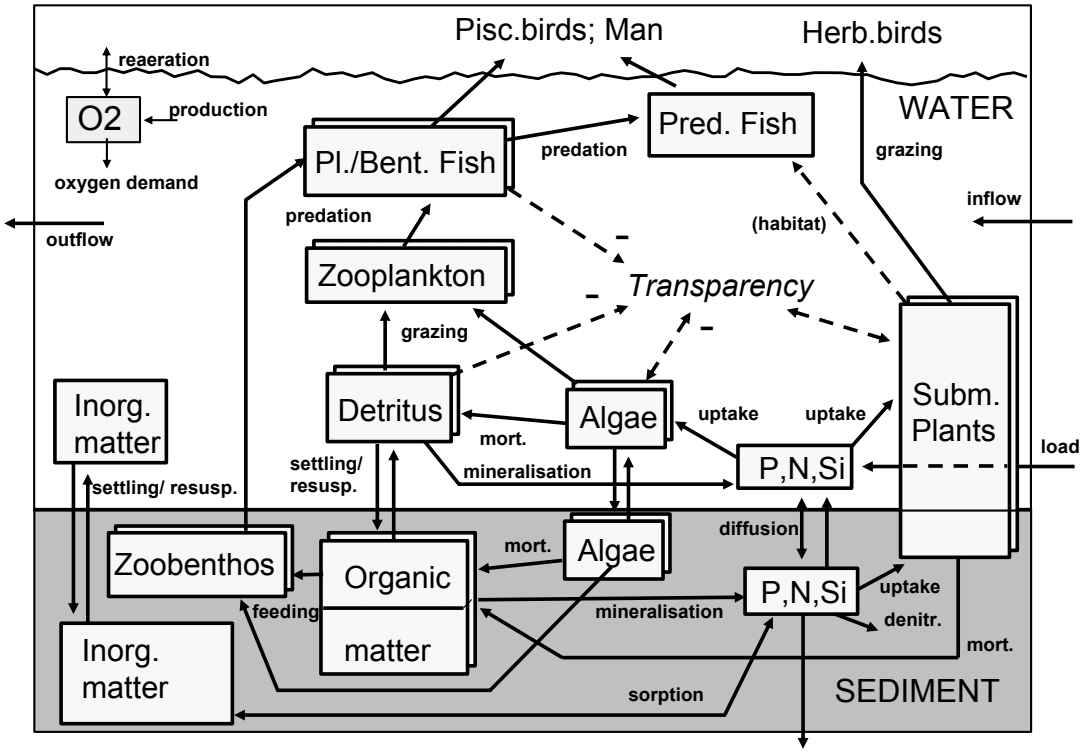
Witteveen+Bos (2010c) Ecologische modellering Loenderveense Plas en Terra Nova. rapport nr. LN4-1-1 (In Dutch)

Wolfer SR, Van Nes EH and Straile D (2006) Modelling the clonal growth of the rhizomatous macrophyte Potamogeton perfoliatus. Ecological Modelling 192:67-82

Yoshida T, Ellner SP, Jones LE, Bohannan BJM, Lenski RE, Hairston Jr NG (2007) Cryptic population dynamics: Rapid evolution masks trophic interactions. PLoS Biology 5:1868-1879

Zadeh LA (1965) Fuzzy Sets, Information and Control 8:338–353

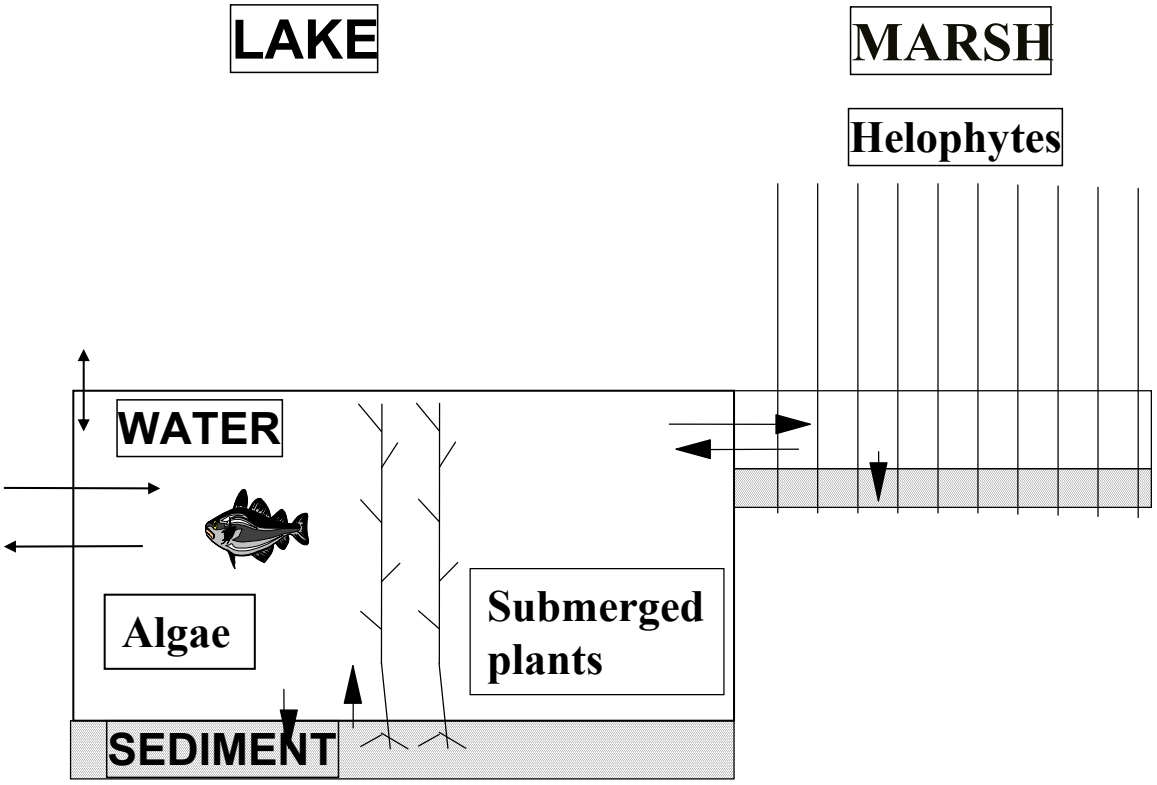
Zhang J, Gurkan Z, Jørgensen SE (2010) Application of eco-exergy for assessment of ecosystem health and development of structurally dynamic models. Ecological Modelling 221:693-702



2089

2090 Figure 1: Overview of the main biotic and abiotic components in the open water module of
2091 PCLake. Compartments are modelled in multiple components (dry weight as a surrogate for
2092 carbon, phosphorus and nitrogen, diatoms and detritus also in silicon). The group Algae is
2093 split in three functional groups: cyanobacteria, diatoms and other small edible algae. The
2094 group Plantivorous/Benthivorous Fish consists of a juvenile, zooplanktivorous and an adult,
2095 benthivorous subgroup. Solid arrows represent transfer of matter, dashed arrows represent
2096 functional relationships that do not involve transport of matter.

2097



2098

2099 Figure 2: Schematic model structure of PCLake including spatial structure. Arrows denote

2100 transport or exchange of matter between spatial compartments. Water level is modelled

2101 dynamically.

2102

Table 1: An overview of model components

Model name[1]	VOL	CEQ[2]	D3D[2]	CAE[2]	MYL[2]	PCL[2]	SHR[2]	IPH[2]	PRO[2]	SAL[2]	[3]	CHA[2]	PIS[2]	[3]	[3]
Category as defined in this paper[4]	STA	CDN	CDN	CDN	CDN	CDN	CDN	CDN	CDN	CDN	MDN	IBM	IBM	S/PM	TBM
Spatial dimension[5]	0-D	2-DV	3-D	1-DV 3-D	1-DV	1-DV 1-DH	1-DV	3-D	1-D	1-DV	0-D	2-DH	0-D	0-D	0-D
Stratification	-	+	+	+	+	-	+	+	-	+	-	-	-	-	-
Sediment	-	+	+	+	+	+	-	+/-	-	+	-	+	-	-	-
Littoral zone	-	-	-	+	-	+	-	-	-	-	-	-	+	-	-
# Phytoplankton groups	0	3+	3-6	7	1	3	2	3	10	2-10	1-3	0	0	0	1
# Zooplankton groups	0	3+	1-3	5	0	1	1	1	1	1		0	1	1	1
# Benthic groups	0	0	1	6	0	1	1	1	0	0		0	1		
# Fish groups	0	0	0	3	0	3	0	3	0	0		1	±8	1-2	1
# Macrophyte groups	0	3+	0	1	0	1	0	1	0	0		±5	0	0	0
# Bird groups	0	0	0	0	0	0-1	0	0-1	0	0		1	3	0	0
Hydrodynamics	-	+	+	+	+	+/-	+	+/-	+/-	+	+/-	-	-	-	-
Temperature dynamics	-	+	+	+	+	+	+	+	+/-	+	+/-	+/-	+/-	+/-	+/-
Oxygen dynamics	-	+	+	+	-	+	+	+	-	+	-	-	-	-	-
CO_2/DIC dynamics	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-
DOC/POC dynamics	-	+	+	+	-	+	+	+	-	+	-	-	-	-	-
Microbial dynamics	-	+	+	+	-	+/-	+/-	+/-	-	-	-	-	-	-	-
P loading	+	+	+	+	+	+	+	+	+/-	+	+/-	+/-	+/-	+/-	+/-
N loading	+	+	+	+	-	+	+	+	+/-	+		+/-	+/-		
Internal P dynamics	-	+	+	+	+	+	+	+	+	+	-	-	-	-	-
Internal N dynamics	-	+	+	+	-	+	+	+	+	+	-	-	-	-	-
Internal Si dynamics	-	+	+	+	-	+/-	-	+/-	-	-	-	-	-	-	-
Sedimentation/resuspension	+	+	+	+	+	+	+	+	+	+	+/-	-	-	-	-
Diagenesis	-	+/-	+	+	-	+/-	-	-	-	-	-	-	-	-	-
Fisheries	-	-	-	+/-	-	+	-	-	-	+/-	+/-	-	+	+	+
Dredging	-	-	+	-	-	+	-	-	-	-	-	-	-	-	-
Mowing	-	-	-	-	-	+	-	-	-	-	-	+	-	-	-

+: fully covered; +/- partially covered; -: not covered; [1] VOL: Vollenweider; CEQ: CE-QUAL-W2; D3D: DELFT3D-ECO; CAE: DYRESM-CAEDYM (1-DV) and ELCOM-CAEDYM (3D); PCL: PCLake (0-d) and PCLake/DUFLOW (1-DH); SHR: Lake Shira Model; IPH: IPH-TRIM3D-PCLAKE; PRO: PROTECH; SAL: SALMO; CHAR: CHARISMA; PISC: PISCATOR; [2] Checked by model developer; [3] These columns do not refer to a specific model but to a group of models instead. [4] Category abbreviations: STA: Static model; CDN: Complex Dynamic; MDN: Minimal Dynamic; SIB: Super-Individual-Based; S/PM: Stage-Structured and Physiologically Structured; TBM Trait Based; [5] Spatial dimension abbreviations: 0-D: 0 dimensional; 1-DV: 1 dim. vertical; 1-DH: 1 dim. horizontal; 2-DV: 2 dim. vertical; 3-D: 3 dimensional

Table 2: An overview of model characteristics (see table 1 for model and category abbreviations.

Model name[1]	VOL	CEQ[2]	D3D[2]	CAE[2]	MYL[2]	PCL[2]	SHR[2]	IPH[2]	PRO[2]	SAL[2]	[3]	CHA[2]	PIS[2]	[3]	[3]
Category as defined in this paper[4]	STA	CDN	CDN	CDN	CDN	CDN	CDN	CDN	CDN	CDN	MDN	IBM	IBM	S/PM	TBM
Mathematical format[5]	RGR	PDE	PDE	PDE	PDE	ODE	PDE	PDE	ODE	PDE	O/PD	DIF	DIF	O/PD	O/PD
Checks on mass balances	+/-	+	+	+	+	+	+	+	-	+	+/-	-	-	+	+
Applies an optimization criterion	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Sensitivity analysis performed		+	+	+	+	+	+	+	+	+		+	+		
Calibration has been performed	+	+	+	+	+	+	+	+	+	+		+	+		
Uncertainty analysis has been performed	-	-	-	+/-	+	+	+	-	-	+		+	-		
Suitable for bifurcation analysis	-	-	-	-	+/-	+/-	-	+/-	-	-	+	+/-	+/-	+	+
Suitable for studying eutrophication	+	+	+	+	+	+	+	+	+	+	+	+	+	+/-	-
Suitable for studying climate change	-	+	+/-	+	+	+	-	+	+	+	+	+/-	+/-	+/-	-
Suitable for fisheries studies	-	+	-	+/-	-	+/-	-	+/-	-	+/-	+	-	+	+	-
Suitable for studying biodiversity loss	-	+	-	-	-	+/-	-	+/-	+	-	+/-	+/-	+/-	-	+/-
Suitable for studying adaptive processes	-	-	-	-	-	-	-	-	-	-	+	-	-	+	+
Both fresh and marine applications	-	+	+	+	-	-	-	-	-	-		-	-	+	+
Applied in water quality management	+	+	+	+	+	+	-	-	+	+	+	+	+	-	-
Applied in fisheries management	-	+	-	+/-	-	-	-	-	-	+	-	-	+	+	+
Implemented in which language		FOR	FOR	FOR	MTL	C++	C++	FOR	FOR	C/DEL	GRD	DEL	DEL	C	C/MTL
Model freely available (on request)		+	+/-	+/-	+/-	+	-	+/-	-	+/-		+/-	+/-		
Has graphical user interface		+	+	+	-	+/-	+/-	+	+	+		+	+		
Fully documented in open literature	+	+	-	+/-	+	+	+	-	+/-	-	+	+/-	+/-	+	+
Model code can be changed by user		+	+/-	+/-	+	+/-	+/-	-	-	+/-		-	-		
Structured as an expandable framework		+/-	+	+	+/-	+/-	-	+/-	-	+/-		-	-		

+: fully covered; +/- partially covered; -: not covered; [1,2,3,4] See table 1; [5] RGR: Regression Equation; PDE: Partial Differential Equation; ODE: Ordinary Differential Equation; O/PD: Ordinary or Partial Differential Equation; DIF: Difference Equation